CONSEIL PERMANENT INTERNATIONAL POUR
L'EXPLORATION DE LA MER
CHARLOTTENLUND SLOT – DANEMARK

RAPPORTS

ET

PROCÈS-VERBAUX DES RÉUNIONS

VOLUME CVIII

CONTRIBUTIONS
TO
SPECIAL SCIENTIFIC MEETINGS
1938

EN COMMISSION CHEZ
ANDR. FRED. HØST & FILS
COPENHAGUE

Août 1938

TABLE OF CONTENTS

Part I

Rate of Growth

Preface ..... I, V
Introduction by Johan Hjort and A. Bückmann ..... I, VII
Contributions:
1. Johan Hjort: Studies of Growth in the North-Eastern Area .... I, 1
2. Per Ottestad: Notes on Statistical Methods of Growth Studies.. I, 9
3. Einar Lea: A Modification of the Formula for Calculation of the Growth of Herring ..... I, 13
4. Per Ottestad: On the Relation between the Growth of the Fish and the Growth of the Scales ..... I, 23
5. Oscar Sund: On Diversity of Growth in Fish ..... I, 33
6. Gunnar Rollefsen: Changes in Mean Age and Growth-Rate of the Year-Classes in the Arcto-Norwegian Stock of Cod ..... I, 37
7. L. Fage et A. Veillet: Sur quelques Problèmes Biologiques liés à l'Etude de la Croissance des Poissons ..... I, 45
8. Erik M. Poulsen: On the Growth of the Cod within the Transition Area ..... I, 49
9. Erik M. Poulsen: On the Growth of the Baltic Plaice ..... I, 53
10. Michael Graham: Growth of Cod in the North Sea and Use of the Information ..... I, 57
11. K. A. Andersson: A Study of the Rate of Growth of some Fishes in the Baltic ..... I, 67
12. A. Bückmann: Über das Wachstum der Nutzfische im Gebiet der Südlichen Nordsee ..... I, 73
13. K. A. Andersson: An Investigation into the Alterations in the Growth-Rate of the Haddock ..... I, 85
14. Arvid R. Molander: Investigations into the Growth-Rates of the Common Dab and the Flounder in the Southern Baltic ..... I, 89
15. Aage J. C. Jensen: The Growth of the Plaice in the Transition Area ..... I, 103
16. Aage J. C. Jensen: Factor determining the Apparent and the Real Growth ..... I, 109

Part II

Light Measurements

1. H. H. Poole: The Effect of Surface Conditions on the Intensity and Angular Distribution of Submarine Daylight ..... II, 3
2. Hans Pettersson: Measurements of the Angular Distribution of Submarine Light ..... II, 7
3. Michael Graham: Trial of Methods of Measuring Transparency of Sea Water ..... II, 13
4. E. K. Gabrielsen und E. Steemann Nielsen: Kohlensäureassimilation und Lichtqualität bei den Marinen Plankton-diatomeen. (Vorläufige Mitteilung) ..... II, 19

Part III

Salmon Migrations

1. Knut Dahl: A Review of Recent Salmon Marking Experiments in Norway ..... III, 3
2. W. J. M. Menzies: Some Preliminary Observations on the Migrations of Salmon (*Salmo salar*) on the Coasts of Scotland .... III, 17

CONSEIL PERMANENT INTERNATIONAL POUR
L'EXPLORATION DE LA MER
CHARLOTTENLUND SLOT, DANEMARK

RAPPORTS

ET

PROCÈS-VERBAUX DES RÉUNIONS

VOLUME CVIII

PART I

RATE OF GROWTH

EN COMMISSION CHEZ
ANDR. FRED. HØST & FILS
COPENHAGUE

Août 1938

CONTENTS

Preface V

Introduction by Johan Hjort and A. Bückmann VII

Contributions:

1. Johan Hjort: Studies of Growth in the North-Eastern Area 1
2. Per Ottestad: Notes on Statistical Methods of Growth Studies 9
3. Einar Lea: A Modification of the Formula for Calculation of the Growth of Herring 13
4. Per Ottestad: On the Relation between the Growth of the Fish and the Growth of the Scales 23
5. Oscar Sund: On Diversity of Growth in Fish 33
6. Gunnar Rollefsen: Changes in Mean Age and Growth-Rate of the Year-Classes in the Arcto-Norwegian Stock of Cod 37
7. L. Fage et A. Veillet: Sur quelques Problèmes Biologiques liés à l'Etude de la Croissance des Poissons 45
8. Erik M. Poulsen: On the Growth of the Cod within the Transition Area 49
9. Erik M. Poulsen: On the Growth of the Baltic Plaice 53
10. Michael Graham: Growth of Cod in the North Sea and Use of the Information 57
11. K. A. Andersson: A Study of the Rate of Growth of some Fishes in the Baltic 67
12. A. Bückmann: Über das Wachstum der Nutzfische im Gebiet der Südlichen Nordsee 73
13. K. A. Andersson: An Investigation into the Alterations in the Growth-Rate of the Haddock 85
14. Arvid R. Molander: Investigations into the Growth-Rates of the Common Dab and the Flounder in the Southern Baltic 89
15. Aage J. C. Jensen: The Growth of the Plaice in the Transition Area..103
16. Aage J. C. Jensen: Factors determining the Apparent and the Real Growth 109

PREFACE

At the meeting of the International Council for the Exploration of the Sea in 1937, the following Recommendation was made by the Consultative Committee and passed by the Council:

> "The Consultative Committee requested the Chairmen of the several Area Committees to prepare short reports summarizing what is actually known about the rate of growth of the principal food fishes in their area and indicating their views as to the conditions which determine the growth. The reports to be considered at a Special Scientific Meeting next year."

In answer to this request the sixteen contributions of this volume were received, some, however, so late that it would not have been possible to study the papers properly prior to the Special Scientific Meeting held on May 26th, 1938. At the first sitting of the Consultative Committee during the 1938 Council Meeting — on May 25th — the Chairman, Professor Hjort, and Dr. A. Bückmann were requested to summarize the contents of the contributions to the Special Meeting in order that everybody interested might be given ample time for a minute study of the information compiled and the views given in relation to the question of growth in course of 1938—39 — and to enable them to add further information or to prepare further views for a discussion to take place at the Council Meeting in 1939.

The summaries prepared accordingly by Professor Hjort and Dr. Bückmann are published as an Introduction to the Volume; Dr. Bückmann's summary specially dealing with the views of the contributions while Professor Hjort's summary is shaped as "General Ideas" on the important question of growth-rate.

After a short discussion it was agreed to postpone the meeting until next year in order to give all members time for the study of the contributions from the different areas, and to recommend

> "That the subject for the Scientific Biological Meeting next year should be the study of the relation between catch and intensity of fishing discussed both from a theoretical and a practical standpoint."

The contributions have not been arranged in any special order — neither as to area nor species —; they are published as to order of receipt from the authors.

Administrative Secretary.

INTRODUCTION

BY

JOHAN HJORT AND A. BÜCKMANN.

GENERAL IDEAS

BY

JOHAN HJORT.

OM all the various areas of the wide sphere f our international co-operation valuable ontributions have been made to the promo- the study of the problems of growth and rate. These voluntary activities may be ac- as evidence of the existence of a widespread in the countries co-operating, and a closer of the individual articles reveals a general us of opinion that growth studies can, in es, be taken as the keynote of the problems study of which this Council was formed: dy of the populations of marine animals in elationship to human industries at sea.

m this point of view all the authors of the are equally interested in the growth of as a biological problem, as well as in the nce of growth for the renewal of those ions which form the basis of human indu- This approach to the problem calls to mind eedingly remarkable historical fact, that interest in the study of growth phenomena st connected with the study of populations. all know, M a l t h u s distinguished between ant and a limited, or restricted, growth, and distinction he raised the problem of the ship between growth and the "means of nce", a problem which was re-stated many ater by C l a u d e B e r n a r d in the terms life of an organism within its specific milieu vironment. The experimental work of u r and L i e b i g — to mention only the tstanding pioneers — paved the way for all ievements in modern times of biochemistry, ental agriculture, medicine, and also of the ience which we are in the process of g, the science of marine biology.

ll these branches of natural science we can a common method of procedure, beginning investigation of the manifold factors which influence the development and fate of individual living beings, followed by the discovery of the specific influence of a physical, chemical, biological, or industrial character which, in special circumstances, may change the course of events, the rate of growth of individuals or populations, and which, therefore, was styled by L i e b i g the "master reaction", the condition which, in a given situation, causes and controls the events in the living world, "la manifestation vitale", to use the words of C l a u d e B e r n a r d.

Of great general interest are the modern discoveries of biochemistry, according to which growth must be considered as a result of balanced reactions between the organism or the population and the factors of the environment. In addition to the means of subsistence we must also take into account the influence of the organism on the structure of the environment. The density of the population may affect the growth of the individuals and thereby the average growth of the population. These important conceptions and discoveries lead us to the new understanding of the balanced reactions between two or more populations of different species. A special case of this general experience is the dependency of a h u m a n population on populations of plants or animals which, by their annual renewal, fulfil the human needs. Most interesting is a comparison of the mathematical symbols which illustrate, on the one hand, the growth of a population of organisms, such as bacteria or yeast cells, in a limited environment, the effect of which may be symbolized by their r a t e o f g r o w t h, and, on the other, the growth of a human industry based on the catch of animals in all those cases in which the human activity is the dominant factor and therefore, by its excessive increase, may use up its own means of subsistence and thus even seal its own deathwarrant. By

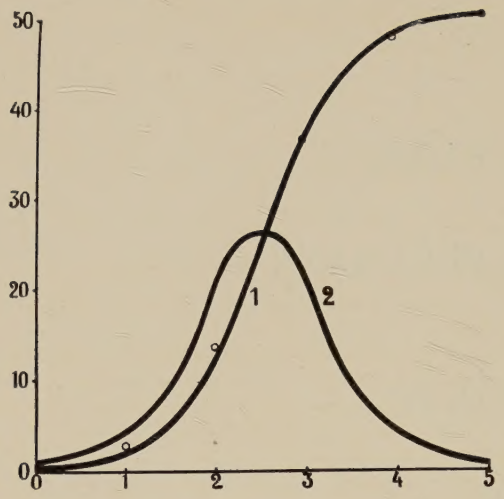


Fig. 1. The sigmoid curve: 1, growth of a colony of bacteria under limited conditions 2, rate of growth.

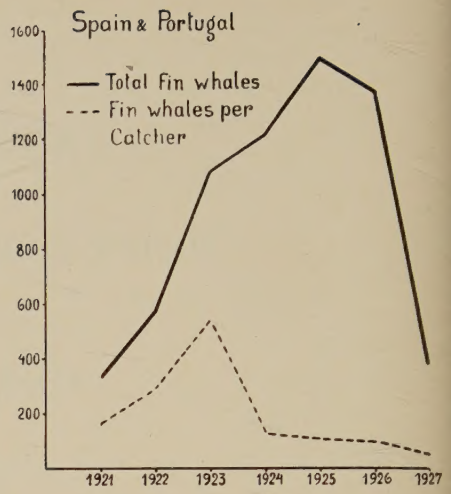


Fig. 2. Fluctuations in the number of fin whales caught off the coast of Spain and Portugal: Solid line — total number of fin whales. Broken line — fin whales per catcher.

comparing two Figures (Figs. 1 and 2) we may demonstrate the analogy between a growth in a limited environment (of bacteria) and the expansion of a human activity (whaling) dependent on a limited population of animals. This comparison of events in nature (Fig. 1) and the fate of a human industry (Fig. 2) leads us to the fundamental and general idea of an o p t i u m c a t c h, the state of affairs in which the dominant factor is the increase of the human population, which must adjust itself to a limited growth, if a lasting situation, an equilibrium, a permanent human activity, is ever to be attained.

The scientific elucidation of this relationship between human activity and the wealth of nature is certainly of the greatest human value. It illustrates what M a l t h u s called the prescribed bounds, the limited possibilities which all men instinctively expect to be faced with in their work.

Of no less importance is the scientific experience of such reactions between the activities of man and nature, where the deciding factor hides in the natural events which are independent of, or very little influenced by, any effort on the part of the human population. The investigations of the coastal fisheries in the North-Eastern Area proved some 30 or 40 years ago that the enormous fluctuations which had taken place for centuries in the fisheries in these waters were independent of the activities of the fishermen. The statistics of the Norwegian cod and herring fisheries of the last decades of the nineteenth century illustrate the truth of this statement by the enormous fluctuations which they reveal in the catches of the fishermen, and also in the number of the fishermen themselves, who

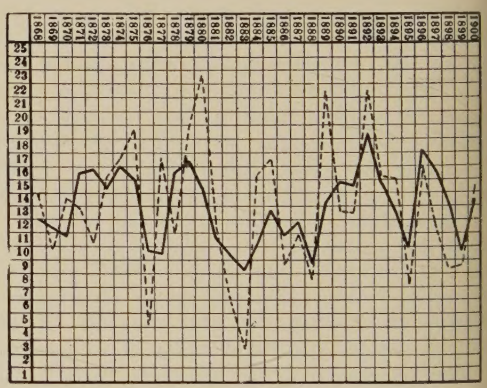


Fig. 3. Cod Fisheries off Northern Norway, 1868—1900. Broken line — number of cod in millions. Solid line — number of fishermen, in thousands.

were compelled to adjust themselves numerically to natural events (Fig. 3).

The final victory of the revolutionary point of view, that these statistics really correspond with or symbolize, events in nature, or that the fluctuations in the catches of the fishermen undoubtedly have their origin in fluctuations in the stock, was attained on the introduction of the system of analysis of the age and growth of the fish in the catches. A comparative study of the age of the fish within the year-classes led to the possibility of a prognosis based on the experience of the conformity within the length of life of the differen

-classes when independent of human activities. n the success of such a prognosis the value of e biological methods for the study of popula- s would appear to have been experimentally fied.

The fact that the fluctuations in the relative ber of the different year-classes have been onstrated as parallel or contemporary in wide s is of the greatest practical importance for creation of a general method, adapted to the y of the effect of human influence on the ity of populations in the sea. In the North- ern Area, where a number of growth-types may distinguished within the large field of distri- on of the herring and cod populations, the uation in the relative strength of the year- es was found to correspond in time within the le field from the south-western to the north- rn parts of Norway, and as far as the herring ulation is concerned this correspondence was demonstrated in Canadian waters. A similar ltaneity of fluctuations in the different had- populations of the northern North Sea was onstrated by the interesting work of H a r o l d o m p s o n[1]).

Compared with this experience growth appears very different problem. While the study of uations may extend over wide areas, that of th demands a material of individuals collected n the most restricted environment. The aim of research must be to describe as closely as pos- the area within the sea in which a uniform th, a uniform type of growth, may be ob- d in all the individuals belonging to the same ies within the area. In all the contributions h have been submitted to this meeting, from areas this view has been maintained either in ral terms or in actual descriptions of charac- tic types of growth. From the Southern North the Belts, the Baltic, Iceland, the Norwegian al waters, most striking examples have been ed of variations of growth from one part of sea to another. And it may be considered of t interest for the study of our methods of rch that the statement is often made that the f i c u l t i e s of attaining to a general under- ling of the growth phenomena have more than been ascribed to the fact that the fish in the moves from one environment to another. Even ing experiments must therefore be considered equate for the problem of obtaining an exact re of the changing influences to which the als in the sea may be exposed by their zontal and vertical movements during the rent periods of their life. For this reason a parison between the growth of animals in the and that of plants on the land, such as trees. been suggestive and confirmed the general iction of a close correspondence between the growth of all organisms and their environments. Most remarkable are the analogies between the changes in the rate of growth, on the one hand of plants under experimental cultivation of the soil, and on the other of fish like the salmon and trout, which are known to move from the one kind of environment to the other.

From these general observations the following c o n c l u s i o n s may de drawn regarding the m e t h o d s of marine biology:—

While growth problems demand a material from the most restricted or uniform environments, the study of the composition of the stock with regard to its year-classes may be extended over wide areas. Through a combination of the study of growth and of age composition in the catches of the fishermen the discovery has been made that t h e s p a w n i n g s h o a l s consist of a great number of different types of growth, which therefore may all be considered as belonging to a common stock or population. In spawning areas specific in their geographical location this heterogeneous population creates the new generations or broods, the individuals of which will be dispersed over a multitude of minor environments and therefore be exposed to a great variation of important physical, chemical and biological factors which will decide their individual rates of growth.

It is evident that the study of t h e i n f l u e n c e o f f i s h i n g on the stock or population of marine animals will require observations extended throughout a series of years. Growth studies within a limited area may in this way illustrate the changes of growth in correlation with the density of the individuals as influenced by the catches of the fishermen. Statistical studies of material, preferably collected from the spawning shoals, and based on length measurements or weights, and amplified by age analyses of minor representative samples, may illustrate the changes in the average mortality within the population in correlation with variations in the intensity or effectivity of the fishing operations within the area of distribution of the population under observation.

In his report on "Fluctuations in the North Sea Haddock Stock" H a r o l d T h o m p s o n[2]) states that "more than three-quarters of the original numbers of a brood seems to be removed before the end of the fourth year. No reserve of older fish is allowed to accumulate to tide over bad times". Similar experience is made in several other areas of the sea, and in recent years signs of the growing influence of fishing on the average mortality of the cod populations have now even been reported[3]) from the North-Eastern Area.

The Haddock of the North-Western North Sea. Rapp. oc.-Verb., Vol. LII, 1928.

[2]) Rapp. et Proc.-Verb., Vol. LXV, 1930.

[3]) See the following contributions from the different areas.

ÜBER METHODIK, ERGEBNISSE UND AUSWERTUNG DER WACHSTUMSUNTERSUCHUNGEN AN NUTZFISCHEN.

VON

A. BÜCKMANN,
Helgoland.

ZUR Diskussion über die Wachstumsverhältnisse der Nutzfische, die auf der Jahresversammlung der Internationalen Meeresforschung in Kopenhagen in der wissenschaftlichen Sitzung am 25. Mai 1938 stattfand, ist eine grosse Zahl von wertvollen Beiträgen eingeliefert worden. Es bestand daher das Bedürfnis, einen Überblick über den wesentlichen Inhalt dieser Beiträge zu gewinnen. Zu diesem Zweck wurde der Verfasser beauftragt, auf der wissenschaftlichen Sitzung eine kurze Zusammenfassung, gegliedert nach einigen wenigen beherrschenden Gesichtspunkten, zu geben. Gemäss dem Vorschlag des Consultative-Committee soll diese Zusammenfassung auch an dieser Stelle zum Abdruck kommen. Sie ist nicht als vollständiges Referat der folgenden Arbeiten anzusehen, sondern soll nur die Punkte herausstellen, deren weitere Erörterung besonders wichtig ist.

Bei der Abfassung der Berichte über das Wachstum der Nutzfische haben offenbar alle Berichterstatter vor einer Reihe von Fragen gestanden, die sich leicht in drei Gruppen zusammenfassen lassen. Es handelt sich erstens um das Problem der richtigen Ermittlung der Wachstumsverhältnisse; zweitens um das Problem der Bedingungen, die das Wachstum bestimmen und regeln, und die insbesondere die örtlichen und zeitlichen Unterschiede im Wachstum der gleichen Fischart verursachen; drittens aber um das Problem, wie wir die Kenntnisse über das Wachstum der Nutzfische für die praktischen Fragen der Fischereiforschung ausnutzen können.

1. Die Ermittlung der Wachstumsverhältnisse.

A. Die Methoden und ihre Mängel.

Unsere Methode der Wachstumsbestimmung ist eng mit der der Altersbestimmung verknüpft. Wir bestimmen, entweder direkt oder auf dem Umweg über die Messung des Wachstums der Schuppen, das dem des Körpers etwa proportional ist, die Durchschnittslänge der Fische in bestimmtem Alter. Nur bei wenigen Fischarten kann daneben die Methode der Wachstumsbestimmung nach dem Zuwachs markierter und wiedergefangener Fische verwendet werden. Beim Kabeljau der Nordsee hat Graham sie — wegen der Unsicherheit der Altersbestimmungen bei diesem Objekt — in Verbindung mit dem Studium der Grössenzusammensetzung des Bestandes weitgehend heranziehen müssen. Bei der Scholle kann sie jedenfalls zur Nachprüfung der auf Altersuntersuchungen gegründeten Befunde dienen.

Alle diese Methoden haben bekanntlich ihre Fehlerquellen, die auch in die aus ihnen abgeleiteten Wachstumsbestimmungen eingehen.

1. Die Altersbestimmungen z. B. können, wie in einzelnen Fällen systematisch nachgeprüft, keineswegs bei allen Individuen sicher und von verschiedenen Untersuchern übereinstimmend ausgeführt werden.

2. Die Methode, das Körperwachstum auf Grund des Schuppenwachstums zu berechnen, ist erheblicher Kritik ausgesetzt gewesen, und ein umfangreiches Schrifttum ist darüber entstanden. Da, wo die Methode sich als anwendbar erweist, bringt sie grosse Vorteile mit sich. Ottestad kommt in seiner Erörterung über die Beziehung zwischen dem Wachstum des Körpers und dem der Schuppe zu dem Schluss, dass dies Problem noch nicht endgültig gelöst ist. Er findet aber, dass Leas Methode bei wirklich homogenem Material des norwegischen Herings sehr wohl ohne wesentlichen Fehler angewendet werden kann. Lea selbst erkennt in seinem Beitrag an, dass das Wachstum von Körper und Schuppe nicht völlig in linearer Proportion erfolgt. Er gibt aber eine Methode an, einen Korrektionsfaktor zu

eln, dessen Einführung die Ergebnisse brauchacht. Nach Jensen besteht bei der Kliesche *ronectes limanda)* kein lineares Verhältnis en dem Wachstum des Fisches und dem des nen. Doch kann man ein solches zwischen der des Otolithen und dem Logarithmus örperlänge annehmen und das Wachstum auf Grundlage berechnen.

Auch bei der Bestimmung des Zunses markierter Fische gibt es rquellen. Erinnert sei nur an das Schrumpfen sche bei Austrocknung vor dem Messen. Doch in diesem Falle die Fehlerquellen, die im den Abschnitt behandelt werden sollen, sicher rösserer Bedeutung.

B. Fehler der Probenentnahme.

Es ist bekannt, dass unsere Fanggeräte nicht völlig repräsentative en des Bestandes liefern. Weitige Geräte z. B. fangen im Verhältnis zu kleine Fische, und die aus solchem Material neten Durchschnittslängen sind zu hoch. In llerem Masse selektiv bezüglich der Grösse der renen Fische ist das Treibnetz. Es scheint , für Wachstumsbestimmungen beim Hering roben aus engmaschigen Schleppnetzen den zu geben. — Werden Proben aus Marktlungen entnommen, so tritt bei vielen Fischzu der Selektion des Geräts noch die Auslese, r Fischer trifft. Dadurch wird der Fehler vergrössert.

Aber auch der Bestand, der im Meere den ist, ist nach Jensens und Bücks Ansicht nicht völlig repräsenhinsichtlich der Wachstumsgeschwindigkeit. e Fischerei vorzugsweise die bestwüchsigen luen entfernt, muss das Wachstum der Überen jeweils um ein Geringes unter dem n Durchschnitt liegen.

Umgekehrt werden bei den Markungsexperimenten, sofern ein Teil arkierten Fische untermassig war, die schnellgen zuerst gefangen und eingeliefert werden. rden zudem vor allem die Marken solcher bemerkt, die schon marktfähige Grösse t haben. Denn die Untermassigen gehen wie diese den Fischern einzeln durch die und es ist daher ein Zufall, wenn bei ihnen arke wahrgenommen wird.

Besondere Schwierigkeiten erheben sich, wenn Plus- und die Minusvarianten Wachstums sich mehr oder wer voneinander sondern. So rn bei der Scholle der süd-östlichen Nordsee tgewachsenen Individuen früher als die langachsenden in tieferes Wasser ab. Trotz der greichen Untersuchungen, die gerade bei Fisch durchgeführt worden sind, ist es, wie mann zeigt, kaum möglich, das wahre durchschnittliche Wachstum der Schollen in diesem Gebiet zu ermitteln. Das gilt nicht allein für die Durchschnittslängen der Altersgruppen, sondern, wie Jensen klarlegt, auch für die Bestimmung des Zuwachses markierter Schollen. Es dürften z. B. im Hornsriffgebiet, wo auf den steinigen Aussengründen beiweitem nicht soviel gefischt wird wie in Küstennähe, mehr von den langsamwüchsigen als von den schnellwüchsigen Schollen wiedergefangen werden.

5. Eine andere Art von Schwierigkeiten finden wir z. B. bei den Heringen des ostanglischen Gebiets (Vergl. Hodgsons Mitteilung in Bückmanns Bericht). In diesem Gebiet kommen Abkömmlinge aus zeitlich und örtlich verschiedenen Laichprozessen miteinander vermischt vor. Sie unterscheiden sich, wo nicht in der Wachstumsgeschwindigkeit, so doch im Alter, dass sie zur gleichen Jahreszeit haben: Die Abkömmlinge des Laichens im Downsgebiet sind jeweils etwa 3—4 Monate jünger als die des Laichens im Bereich von Doggerbank und Yorkshireküste in der gleichen "Altersgruppe". Es ist eine einleuchtende Annahme Hodgsons, dass innerhalb jeder Altersklasse die früher geborenen Individuen im Durchschnitt grösser sind als die später geborenen, und dass daher die Durchschnittslänge eines Jahrgangs sich von der eines anderen im gleichen Alter unterscheiden kann, je nachdem der Anteil der beiden Gruppen an den Jahrgängen verschieden ist. — Ob diese Auffassung zutrifft, wird man wohl am besten klären können, wenn es gelingt, nach der von Erdmann entwickelten Methode die Angehörigen der beiden Gruppen auf Grund des Otolithenbildes individuell voneinander zu trennen.

Wenn hier ein Überblick über die Schwierigkeiten und Fehlerquellen der Wachstumsbestimmungen versucht wurde, so soll das doch keineswegs den Eindruck erwecken, als seien die Ergebnisse der bisher geleisteten Arbeit nicht verlässlich oder gar wertlos. Der Zweck ist vielmehr, zu kritischem Vorgehen, insbesondere zu Untersuchungen über die Grössenordnung der entstehenden Fehler, anzuregen. Bei unseren Arbeiten auf dem Gebiet der Fischereiforschung sind wir nur selten in der glücklichen Lage, theoretisch von vornherein beweisen zu können, dass unsere Methoden unanfechtbar seien. Wir sind vielmehr darauf angewiesen, die Methoden zunächst einmal praktisch anzuwenden und dann zu prüfen, ob die erzielten Ergebnisse sinnvoll sind und einander stützen und bestätigen. Tun sie das, so ist die Methode brauchbar, und das ist auch bei den Wachstumsuntersuchungen im wesentlichen der Fall. Schon die Feststellungen über die zeitlichen und örtlichen Verschiedenheiten des Wachstums der Nutzfische und ihre Ursachen, von denen im folgenden die Rede sein soll, lassen uns das erkennen.

2. Die Bedingungen, die das Wachstum bestimmen.

Wenn wir beobachten, dass Fische der gleichen Art in verschiedenen Gebieten, oder gar in ein und demselben Gebiet zu verschiedenen Zeiten, verschiedene Wachstumsgeschwindigkeit aufweisen, so stellt uns das vor die Frage, welche Faktoren denn das Wachstum bestimmen und jeweils durch ihren Einfluss diese Unterschiede hervorrufen. Wir wissen, dass die Bedingungen des Wachstums z. T. in dem Fisch selbst liegen, in seiner Erbanlage und in seinem physiologischen Zustand, z. T. aber auch in der Beschaffenheit des Lebensraumes, der ihn umgibt.

A. Innere Faktoren.

1. Strodtmann bezeichnet in seiner interessanten Studie über das Wachstum der Ostseeschollen (5) die ererbte Fähigkeit des Fisches zu wachsen als sein *"potentielles Wachstum"*. Er beweist, dass sich diese Erbanlage nicht ändert, auch wenn die Fische eines Bestandes durch viele Generationen hindurch durch die Beschaffenheit ihres Lebensraumes an der Entfaltung ihres potentiellen Wachstums gehindert werden. Wir dürfen annehmen, dass das potentielle Wachstum innerhalb eines einheitlichen Bestandes, einer Laichgemeinschaft, im allgemeinen gleich ist. Das gilt also etwa für den gleichen biologischen Bezirk, für den nach Hjort die Fluktuationen in der Stärke der Jahrgänge gleichsinnig verlaufen. Das realisierte Wachstum aber kann innerhalb dieses Bezirks sehr verschiedenartig sein. —Andererseits zeigen die in Jensens Bericht erwähnten Befunde Blegvads, dass verschiedene Bestände der gleichen Fischart sich im potentiellen Wachstum unterscheiden können: Markierte baltische Schollen wuchsen in der Beltsee langsamer als die dorthin verpflanzten Nordseeschollen.

2. Strodtmann hat in der erwähnten Arbeit weiter gezeigt, dass das potentielle Wachstum der Fische in Abhängigkeit von ihrem physiologischen Zustand vermindert wird, und zwar in gewissem Umfang wohl mit zunehmendem Alter, vor allem aber mit dem Eintritt der Geschlechtsreife, die ja den Baustoffwechsel des Fisches vom Aufbau von Körpersubstanz auf den Aufbau von Fortpflanzungskörpern umlenkt. Den hemmenden Einfluss der Geschlechtstätigkeit auf das Wachstum können wir bei vielen Fischarten ohne weiteres an der Wachstumskurve ablesen: Der Jahreszuwachs vermindert sich in dem Alter, in dem die Geschlechtsreife eintritt, plötzlich sehr stark. Wie Fage und Veillet mitteilen, ändern sich parallel mit der Entwicklung der Geschlechtsorgane in manchen Fällen auch die Proportionen des Wachstums. — Wenn ferner bei sehr vielen Fischarten die Männchen langsamer wachsen und eine geringere Höchstlänge erreichen als die Weibchen, so ist dies wahrscheinlich zumeist darauf zurückzuführen, dass die Geschlechtsreife beim ♂ früher im Leben eintritt als beim ♀. Es sei hier nur auf die Angaben im Bericht von Fage und Veillet über den Seehecht *(Merlucius merluccius)*, die Meerbarbe *(Mullus barbatus)*, die Sardine *(Clupea pilchardus)*, den Flügelbutt *(Lepidorrhombus megastoma)* hingewiesen. Andere Beispiele sind leicht zu finden. Es wird interessant sein zu klären, ob auch der von Rollefsen festgestellte Geschlechtsunterschied im Wachstum des Kabeljaus auf früheren Eintritt der Geschlechtsreife beim ♂ zurückzuführen ist. Bei Fage und Veillet sowie bei Poulsen (Kabeljau der Übergangsarea) finden wir ferner Beispiele dafür, dass die Geschlechtsreife in einem Gebiet — wohl ihrerseits unter dem Einfluss der Temperatur — früher eintritt als in einem anderen. Dann wird das potentielle Wachstum früher reduziert, das Wachstum verlangsamt sich entsprechend und strebt einer geringeren Höchstgrenze zu.

B. Die Bedingungen des Lebensraumes.

1. Lernten wir soeben einen indirekten Einfluss der Temperatur mit dem Effekt einer Beschränkung der Körpergrösse kennen, so finden wir im allgemeinen den direkten Einfluss vorherrschend, dass höhere Temperatur, wie ganz allgemein die gesamten Stoffwechselvorgänge, so auch das Wachstum beschleunigt. Wir haben eine Reihe interessanter Beispiele für die Abhängigkeit der Wachstumsgeschwindigkeit von der Temperatur in Tåningş Bericht über die North-Western Area. In diesem Mischgebiet kalter und warmer Wasserkörper ist das Wachstum von Kabeljau, Schellfisch, Scholle, Heilbutt in den wärmeren Teilen stets schneller als in den kühleren.

2. Es ist eigentlich selbstverständlich, dass die Ernährungsverhältnisse die Wachstumsgeschwindigkeit der Fische beeinflussen. Für die Scholle ist dies bereits durch C. G. Joh. Petersen (3) nachgewiesen und praktisch ausgenutzt worden. Er nutzte das schnelle Wachstum der Schollen in den nahrungsreichen, schwach mit Schollen besiedelten inneren Teilen des Limfjords, indem er Schollen von den nahrungsarmen, übervölkerten westlichen Teilen dorthin verpflanzte. — Über regionale Verschiedenheiten des Wachstums, die auf Unterschiede in der Nahrungsmenge zurückzuführen sind, berichtet im folgenden K. A. Andersson. Hering und Kabeljau wachsen im Bottenbusen schneller als in der mittleren Ostsee. Dies kann an sich auch auf andere Bedingungen des Lebensraumes zurückzuführen sein, so auf den Sauerstoffmangel in den Tiefen der mittleren Ostsee, der mit der halinen Schichtung in Verbindung steht. Doch dürfte Anderssons Auffassung zutreffen, dass die unmittelbare Ursache der Verschiedenheit in den Ernährungsverhältnissen zu

en sein, dabei allerdings mit den erwähnten ographischen Verhältnissen mittelbar in Ver- ung stehen dürfte. Die Heringe finden im rnbusen ein besonders reiches Zooplankton. der Kabeljau findet dort bessere Ernährungs- ngungen. Er frisst z. B. hier viel Heringe, end der Dorsch in den Tiefen der mittleren e das nicht kann. Die Heringe halten sich vorzugsweise in der gut durchlüfteten Deck- ht auf.

Ebenso bekannt wie bedeutsam sind die- en Fälle, wo die Ernährungsverhältnisse in n Gebiet sich dadurch verbessert haben, dass Fischbestand durch die Fischerei ichtet und damit die Nahrungskonkurrenz indert ist. Hier ist vor allem die Wachstums- leunigung der Plattfischarten in den Gebieten Kattegat bis zur mittleren Ostsee zu erwähnen gl. Jensen, Molander, Poulsen).

Eine Beschleunigung des Wachstums in den n Jahren weist auch Rollefsen für den eljau der Schelfgebiete des nordöstlichen ntischen Ozeans nach. Nachweislich hat in n Gebiet die Intensität der Fischerei sehr nommen, und man könnte auch hier an Verbesserung der Ernährungsverhältnisse ge der Lichtung des Bestandes denken. Doch nt bezüglich dieses Schlusses Vorsicht geboten. deutschen Untersuchungen des letzten Jahres im ntsmeer erbrachten gewisse Anzeichen dafür, in diesem wichtigen Wachstumsgebiet des sch-norwegischen Kabeljaubestandes die Tem- uren gegenwärtig höher liegen als vor einigen n. Die Wachstumsbeschleunigung der Kabel- könnte also sehr wohl auf diese thermische rung zurückzuführen sein.

Ebenso schwierig ist auch die Frage nach Ursachen des schnelleren Wachs- s des Schellfischjahrgangs 1937 Skagerak im Vergleich zum Jahrgang . Es ist nicht zu bestreiten, dass der Schell- bestand zur Zeit des Heranwachsens des Jahr- s 1928 viel dichter war als gegenwärtig, und t daher durchaus berechtigt, wenn Anders- die Wachstumsbeschleunigung damit in Zu- nenhang bringt. Indessen ist zu berücksichtigen, die erheblichen Schwankungen der Bevölke- sdichte, die die Fluktuationen beim Schellfisch er Nordsee verursacht haben, ohne Wirkung die Wachstumsgeschwindigkeit gewesen sind. rerseits bestehen in verschiedenen Teilen der see sehr bezeichnende Unterschiede in der stumsgeschwindigkeit dieser Fischart, die auf Temperaturverhältnisse zurückgeführt werden. t daher nicht völlig ausgeschlossen, dass die unft der im Skagerak angetroffenen Schell- e massgebend für ihre Grösse in bestimmtem ist.

Dafür, dass auch die durch Fluktua- nen herbeigeführten Bestandsschwankungen Ernährungsverhältnisse beeinflussen und mit Wachstumsschwankungen beantwortet werden können, haben wir ein gutes Beispiel bei den Schollen der südöstlichen Nordsee.

Im Bereich der Jungschollengründe der südöstlichen Nordsee sind die Bodentemperaturen während der sommerlichen Wachstumsperiode der Schollen so hoch, dass unter diesem Gesichtspunkt optimales Wachstum möglich wäre. Dagegen ist die Besiedlung des Meeresbodens mit Nährtieren mit seltenen Ausnahmen gering, und die Jungschollenbevölkerung ist, besonders wenn ein reicher Jahrgang heranwächst, sehr dicht. Da die Scholle zudem in den ersten Lebensjahren keine ausgedehnten Wanderungen ausführt und vergleichsweise wenig beweglich ist, so ist es sehr erklärlich, wenn die auf den einzelnen Fisch entfallende Nahrungsmenge hier der wachstumsbegrenzende Minimumsfaktor wird. Von grossem Interesse ist Jensens Nachweis, dass das Wachstum im Hornsriffgebiet schon von September an erheblich zurückgeht, obwohl die Temperaturen noch bis Ende Oktober optimales Wachstum gestatten würden. Offenbar ist der Nahrungsvorrat schon vorher aufgebraucht. In der nahrungsreichen Beltsee dauert nämlich das Wachstum solange an, wie die Temperatur es gestattet.

7. Aus dem Material Thursby-Pelhams, dass in Bückmanns Bericht verwendet ist, geht nun hervor, dass die Unterschiede in der Wachstumsgeschwindigkeit der einzelnen Schollenjahrgänge, die auf den Jungfischgründen der südöstlichen Nordsee beobachtet worden sind, sich in der ganzen südlichen Nordsee fühlbar machen, obwohl die küstenferneren Gebiete nahrungsreich und nur dünn mit Schollen besiedelt sind. Dies erklärt sich wohl wie folgt: Die Abwanderung der Schollen von den Jungfischgründen ist in erster Linie von der erreichten Grösse, weniger von dem Alter abhängig. Die langsamwachsenden Jahrgänge bleiben daher länger in dem nahrungsarmen Gebiet, und zwar zu einem nicht geringen Teil bis zum Alter von 6 Jahren. In diesem Alter steht der Eintritt der Geschlechtsreife mit seinem wachstumshemmenden Einfluss auch bei schlecht gewachsenen Schollen schon nahe bevor. Daher vermögen diese Schollen auch nach Abwanderung auf die nahrungsreichen Aussengründe ihren Rückstand im Wachstum gegenüber den schnellwüchsigeren Jahrgängen nicht mehr aufzuholen.

8. Übrigens scheinen auch bei anderen Fischen Wachstumsschwankungen in Verbindung mit den Fluktuationen in der Stärke der Jahrgänge vorzukommen. So berichtet Tåning von einem Rückgang des Wachstums der Kabeljaus bei Island im Zusammenhang mit dem Auftreten des reichen Jahrgangs 1922, und Poulsen findet ähnliche Verhältnisse in einem allerdings nur kleinen Material von Kabeljaus aus der Übergangsarea.

Dieser Überblick über die Bedingungen, die das Wachstum bestimmen, ist in sich nicht vollständig. Ein eingehenderer Vergleich der in den verschiedenen Areas beobachteten Wachstumsverhältnisse würde ihn noch wesentlich ergänzen, doch muss diese Aufgabe der Spezialbearbeitung überlassen werden.

Wir haben auch mit dieser Darstellung die Ergebnisse der Wachstumsuntersuchungen überhaupt keineswegs erschöpft, sondern nur den unter einem bestimmten, freilich sehr wichtigen Gesichtspunkt auffallenden Teil der Ergebnisse zusammengestellt. Andere, an sich auch wichtige Befunde konnten nicht der Gegenstand einer zusammenfassenden Darstellung sein. Diese hat sich vielmehr über das Gesagte hinaus vornehmlich mit der Frage zu beschäftigen, wie die gewonnenen Kenntnisse weiterhin nutzbringend verwendet werden können.

3. Die praktische Verwertung der Feststellungen über das Wachstum.

Die Untersuchung der Wachstumsgeschwindigkeit der Nutzfische ist von grösster Bedeutung. Denn ihre Kenntnis ist ein wesentliches Element zur Beantwortung der Frage, welche Art und Stärke der Fischerei auf die Dauer den höchsten Gesamtertrag der befischten Nutzfischbestände gewährleiste. Und dies ist das Kernproblem aller Fischereiforschung.

Der Verfasser hat an anderer Stelle (1) einen Versuch gemacht, deutlich zu machen, wie wichtig die Lösung dieser Frage für uns sein muss und hat zusammengefasst, was in letzter Zeit an theoretischen Erörterungen zur Vorbereitung einer solchen Lösung vorgebracht worden ist. Eine endgültige Klärung der Frage kann allerdings nur durch einen praktischen Versuch erfolgen. Doch ist es nötig, diese Klärung durch Beobachtung und Überlegung vorzubereiten.

1. Wir müssen, wie Russell 1931 (4) klar dargestellt hat, einen möglichst hohen Ertrag der Fischerei anstreben, der nicht nur durch fortgesetzte Verdünnung des Bestandes und durch fortgesetzte Steigerung der Befischungsintensität auf gleicher Höhe erhalten wird, sondern der wirklich näherungsweise konstant ist. Das bedeutet, dass der Fang immer nur der natürlichen Vermehrung des Bestandes entsprechen kann, d. h. dem Überschuss der Nachwuchserzeugung und des Substanzanfalls durch Wachstum über den Abgang durch natürliche Sterblichkeit. Wir müssen annehmen, dass es für jede Stärke der Befischung einen Gleichgewichtszustand zwischen Bestand und Fischerei gibt, für den die Gleichung Russells gilt: Fang gleich Nachwuchs plus Zuwachs minus natürliche Zehrung,

$$C = A + G - M,$$

sodass jeder Befischungsintensität eine bestimmte Grösse des Bestandes und des Fanges entspricht. Es gilt also festzustellen, welcher Befischungsintensität der grösste Fang zugeordnet ist.

Dies auf der Grundlage der Russell'schen Formel zu berechnen ist sehr schwierig, da zwischen der Grösse des Bestandes und den Gliedern der Gleichung sehr verwickelte Beziehungen bestehen. Greifen wir einmal das Glied G heraus, das das Wachstum des Bestandes bezeichnet und daher hier von besonderem Interesse ist: Das Bestandswachstum ist einmal abhängig von der individuellen Wachstumsgeschwindigkeit, von der bisher die Rede gewesen ist. Zum anderen ist es abhängig von der Grösse und Zusammensetzung des Bestandes. Je mehr Fische vorhanden sind, die wachsen können, umso grösser ist natürlich die Gesamtmasse des erzeugten Gewichts. Der Bestand seinerseits ist umso grösser, je schwächer die Befischung ist. Allerdings nimmt das Bestandswachstum nicht im gleichen Verhältnis zu wie die Grösse des Bestandes: Ein sehr grosser, d. h. also schwach befischter Bestand enthält viele alte geschlechtsreife Tiere, und bei diesen ist, wie wir wissen, die individuelle Wachstumsgeschwindigkeit gering. — Zu diesen statistischen Beziehungen kommt noch, dass durch biologische Verknüpfung eine Abhängigkeit der individuellen Wachstumsgeschwindigkeit von der Grösse des Bestandes herrschen kann, wie wir das z. B. bei der Scholle gesehen haben. Hier sinkt die individuelle Wachstumsgeschwindigkeit infolge Nahrungsmangels in allzu dichten Beständen. Diesen verwickelten Beziehungen können wir beim Versuch einer theoretischen Berechnung des Bestandswachstums nicht gerecht werden! — Bei der natürlichen Zehrung und der Nachwuchserzeugung liegen die Verhältnisse keineswegs einfacher.

2. Nun hat man den Verlauf des Wachstums von verschiedenartigen Organismen (Individuen und Beständen), untersucht und hat gefunden, dass dieser in vielen Fällen durch gewisse einfache mathematische Funktionen beschrieben werden kann. Wenn wir die Funktion kennen würden, die das Wachstum eines Nutzfischbestandes beschreibt, so wären wir der Diskussion der Wirkung der einzelnen Faktoren, die wir nicht durchführen können, überhoben, denn die Wachstumskurve trägt ja der Wirkung aller fördernden und hemmenden Faktoren Rechnung. Wir könnten dann aus der ersten Ableitung der Funktion — der Kurve der absoluten Wachstumsgeschwindigkeit — die Lage des Höhepunkts der natürlichen Vermehrung im Verhältnis etwa zur Bestandsgrösse ablesen. Leider gibt es aber kein allgemeingültiges Gesetz des organischen Wachstums. Die Wachstumskurve eines Fischbestandes kennen wir in keinem einzigen Falle und wissen garnicht, durch was für eine Funktion sie approximiert werden könnte. Ohne diese Kenntnis sind alle unsere Schlussfolgerungen haltlos. Es

Funktionen, die Wachstumsvorgänge beschrei-
bei denen die grösste natürliche Vermehrung
itt, wenn der Bestand die Hälfte der maximalen
se erreicht. So ist es bei dem Robertson-
n Gesetz und bei der von Ottestad auf
hstumsvorgänge angewandten Binomialfunk-
Andererseits fanden Fischer und Buch-
Hresen, dass das Wachstum von Explantaten
einer Funktion anglich, bei der die grösste
nehrung schon eintritt, wenn wenig mehr als
Viertel der maximalen Bestandsgrösse erreicht
Man sieht also, dass wir ohne wirkliche
ntnis des Bestandswachstums von Fischen auch
diesem Weg nicht zu verlässlichen Ergebnissen
men.

. Indessen hat Graham (2) eine wohldurch-
te Methode ausgearbeitet, die einen Fortschritt
nserem Gebiet ermöglicht. Freilich vermag er
Problem nicht in seiner allgemeinsten Form zu
, sondern er muss die Fragestellung einengen.
e Frage lautet: Würde sich der Fang auf die
r gesehen vergrössern oder verkleinern, wenn
Befischung der Nordsee soweit eingeschränkt
en würde, dass die Kabeljaus (oder die Schell-
e, oder die Schollen) ein Jahr älter werden
en als heute? Diese Frage kann er beantwor-
wenn er die Hilfsannahmen einführt, dass bei
solchen Verminderung der Fischerei der
wuchsanfall zum wenigsten nicht zurückgeht
dass die individuelle Wachstumsgeschwindigkeit
verändert wird. Dazu kommen ferner einige rechnerische Approximationen, z. B. die Annahme konstanter Geschwindigkeit des Ablaufs von Wachstum und natürlicher Zehrung innerhalb begrenzter Zeiten.

Graham hat unten ein Beispiel seiner Berechnungsweise sehr klar durchgeführt. Es handelt sich dabei um den Kabeljau der Nordsee. Nach dem Ergebnis dieser Berechnung ist die heutige Befischung des Kabeljaubestandes der Nordsee weit stärker, als dass sie den grösstmöglichen Ertrag liefern könnte. Mit anderen Worten: Wenn wir weniger fischen würden, so würden wir nach Verlauf weniger Jahre mehr fangen als heute und zwar mit einem geringeren Aufwand von Betriebsmitteln. Wir würden also mehr und billigeren Fisch haben. Diese Feststellung kennzeichnet hinreichend die grosse Bedeutung unseres Problems und die Wichtigkeit jedes Versuchs zu seiner Lösung.

Notwendig ist jetzt vor allem eine Aussprache über die Berechtigung der von Graham ausgearbeiteten Methode und die Zulässigkeit der von ihm eingeführten Hilfsannahmen und Approximationen. — Ebenso notwendig ist die Verbesserung der Unterlagen für die Berechnung. Das sind vor allem das Bestandswachstum — individuelles Wachstum in Verbindung mit Zusammensetzung und Grösse des Bestandes — und die natürliche Zehrung, über die wir nur ganz unzureichend unterrichtet sind.

Verzeichnis der erwähnten, nicht in diesem Bande enthaltenen Schriften.

ickmann, A. Über den Höchstertrag der Fischerei
d die Gesetze organischen Wachstums. Ber. Deutsch.
iss. Komm. f. Meeresf. N.F., Bd. IX, Heft 1, 1938.

raham, M. Modern Theory of Exploiting a Fishery,
d Application to North Sea Trawling. Journ. du
nseil, Vol. X, 3, 1935.

etersen, C. G. Joh. Report of the Danish
Biological Station, XVIII, 1 und 2, 1909.

4. Russell, E. S. Some theoretical Considerations on the "Overfishing" Problem. Journ. du Conseil, Vol. VI, Nr. 1, 1931.
5. Strodtmann, S. Das Wachstum der Schollen in der Ostsee. Ber. Deutsch. Wiss. Komm. f. Meeresf. N.F., Bd. VII, H. 4, 1935.

1

STUDIES OF GROWTH IN THE NORTH-EASTERN AREA.

BY

JOHAN HJORT.

FOR nearly forty years the International Council has been engaged on the investigation of the conditions of life of those animal populations which, by their annual renewal and growth, support the great sea fisheries of northern Europe. To a very great extent this study in marine biology has been built up on the ideas and methods which the science of population has created for the study of human communities. In the biological study of the effects of human activity on the sea, however, the problems assumed another shape when it became evident that in all those activities which we style hunting and fishing events will not depend merely on the changes, fluctuations or reductions in the number of hunters or fishermen, but also on the magnitude of the stock of living organisms on which the activity is based. We distinguish, therefore, between two different populations. On the one hand there is the human population of hunters, or fishermen, on the other the stock or "populations" of living organisms, and in the simultaneous study of both of these populations, their growth or decline, lies the most important task of the biological science of population, and its application to all problems of marine biology.

The approach to these studies was made by means of the hypothesis which seemed so daring forty years ago, but which, in an increasing degree, has proved so fertile, namely, that the catches of the fishermen can be regarded as representative, relative measures of the then existing stock of those species of fish of which the catches are composed. As a method the application of this hypothesis obtained a considerably enhanced importance, since means were successfully found for determining ages by the study of growth-zones in different organs of the fish, bones, scales or otoliths. By this means the catches of the fishermen could not only be made to yield representative information concerning fluctuations or changes in the size of the fish populations but it was also possible by analysing the age and growth of the fish in the catches to study the movement within the population from year to year. The stock of fish was thus analysed for its composition of year-classes, and in the study of fluctuations in this composition from the one year to the other there arose the conception of changes governed by law, of such a nature as to make definite prognoses possible, and which were confirmed by the experiences of succeeding years. Hence this biological method seems to have received its experimental verification.

A desire has now arisen for discussion of the ideas and experience which must be said to form the foundation of this doctrine of population, namely, our methods of studying growth and growth-rate. This desire I do not regard as indicative of doubt or lack of confidence in the results hitherto achieved. Rather it arises from uncertainty over the question of whether we can probe further into the causative connexion between growth and *milieu*, and set for ourselves new and far-reaching aims. If this opinion of mine is correct our task at this meeting will be, before all, that of studying the question whether there is any vagueness of opinion as to the validity of our theoretical basis or the application of our methods. For this reason it may, perhaps, be expedient to glance briefly at our terminology for the ideas of growth and growth-rate and at the mathematical functions which have been employed to describe or characterize these ideas. In the hope of contributing to an understanding of this Dr. Per Ottestad has drawn up a very brief summary of the terms employed in the literature. This summary is printed in connexion with my presentation of the problems which have been predominant in growth investigations, especially those in the North-Eastern Area.

In various publications I have emphasized that the modern doctrine of population owes its origin to the introduction, by Robert Malthus, of the conception of time, the movement in the study of populations, just as Galileo did in mechanics. But in the formula for the exponential growth $y = m \cdot a^t$ the time unit taken by Malthus was not a quantity chosen at random. It was founded on the biological conception of "the period of duplication" and the formula, therefore, applied to organisms which according to experiment doubled their populations at regular intervals. This

case of the North American pioneers, was ed at 25 years, and in P a s t e u r's experi- studies of the multiplication of yeast- t periods of 15 minutes. This gives rise to the n of whether the formula constructed by h u s can be applied to those types of sms, the reproductive mechanism of which is uished by a progeny of thousands or millions ms in each generation.

ere is another b i o l o g i c a l experience ted with M a l t h u s's formula. It assumes ne surrounding world, the *milieu*, contains ted possibilities for growth throughout a r of generations. In other words, that s", or as M a l t h u s puts it, "restrictive , do not occur in the environment. The new mental biochemistry has succeeded in showing rect that where a constant *milieu* of this kind essfully maintained there also a population st-cells or bacteria can grow according to ponential law of growth. Biochemistry has own that the constants of the *milieu* do not presuppose a surplus of "means of sub- e", but also that the effect of the organisms lves on the *milieu* through their excretion of ducts of metabolism must be removed if the -rate is not to stop or be retarded. Actually, s yet a third assumption which is of an y b i o l o g i c a l nature, and this must not rlooked if the problems of growth are to be ood. This is the growth of the i n d i - a l s within the population. The individuals make up the populations do not grow ng to the exponential law. That their uctive mechanism leads to a definite "dupli- period" is due to the fact that their individual follows an entirely different course and. ally speaking, reaches certain "prescribed " in a l i m i t e d growth. The growth of the tion throughout a number of generations, re, takes place, in reality, in the form of periodic cyclic movements, along the growth

m the very beginning it has been common dge in natural history that in the majority es in the growth of both individuals and ions, a distinct difference in growth-rate observed in the individual periods of the R a y m o n d P e a r l has attempted to e this experience in the following words:— owth occurs in cycles. Within one and the y le, and in a spatially limited area or e, growth in the first half of the cycle starts but the absolute increment per unit of time s steadily s m a l l e r until the end of the

phically, it has been possible to illustrate wth by curves which show, *inter se*, con- e differences but which, however, present characteristic relationship that they can be d under the common designation of S-shaped or sigmoid curves. In the sigmoid growth there is a continually fluctuating g r o w t h - r a t e, first increasing and then decreasing. Many biologists have been occupied with the idea that the increasing numbers of cells or individuals first seem to stimulate each other's growth, and then to retard it. Efforts have been made to find an analogy for this process in the chemical reversible reactions which are symbolized by the sign $\rightleftarrows$ in which, simultaneously, but with fluctuating power or rapidity, certain chemical combinations are formed and again decomposed. The new experience of the influence of the organisms on the composition of the *milieu* has seemed to strengthen this point of view, and in that interesting book "Principles of Biochemistry" T. B. R o b e r t s o n has endeavoured to show, on the assumption that the phenomena of growth can be regarded as autocatalytic reactions, that this theory results in an illustration of the events by a sigmoid curve. In this connexion R o b e r t s o n, P e a r l and R e e d have attempted to develop a mathematical function for sigmoid growth, as Dr. O t t e s t a d has explained more fully in his summary.

According to O t t e s t a d these formulae will have to be regarded as an attempt to adapt a mathematical function to certain phenomena the existence of which has been revealed through experience. And the functions have then been applied to an "extrapolation" beyond experience, e. g., to predictions of future events in the growth of the populations. For this purpose a number of constants are introduced into the functions, and by this means it has become possible to produce an approximate similarity between the constructed constants and those which are found purely empirically. I do not, by any means, wish to dispute or reduce the value of these efforts. They are useful so long as it is borne in mind that they can only be regarded as heuristic, hypothetical methods, and that they cannot postulate anything concerning events abstract from experience.

It is of fundamental or principal importance to biologists to remember that the problems of growth do not lend themselves to representation by any kind of mathematical functions, which, through their constants, should be capable of reflecting the sum total of the factors which control the course of the growth. This would be to arrogate a "complete understanding" of the phenomena of life, or to construct the origin of the organisms. The task must therefore be to present a d e s c r i p t i v e illustration of the course of the events, and it is this which O t t e s t a d has endeavoured to do by taking as a basis the ordinary statistical rules for such graphical illustrations of the statistical experiences and their analysis.

The question then arises: For what purpose can this statistical method be applied in b i o l o g i c a l research? It is my belief that this question can best

be answered if it is viewed in the light of von Liebig's famous Law of the Minimum, the law of the master reaction. The value of this law to the study and understanding of the problems of growth lies in the fact that no attempt is made to disvover all the factors which play a part in the life of the individuals, but that, on the contrary, an effort is made to discover one definite factor or group of factors decisive, in the particular case, for changes in the growth of an individual or population.

Liebig's law, as is well known, was developed for the study and practice of agriculture, and it rested, in reality, on a general conviction that there is an accord between the growth of the organisms and the surrounding *milieu*. Where science can discover and follow the master reaction which, in the particular case, elicits a change in the growth, there it can understand the course of the events. The first step must therefore be, by analysis of the many-sided reality, tentatively to make a selection of the factors which, hypothetically, can be accepted as controlling the events. It is clear that the study of the plants growing on the land has this advantage that these organisms can be observed throughout their lives and that, therefore, the correlation of growth and a particular *milieu* can be constantly controlled. The organisms in the sea, on the other hand, are continually in motion during their lives and can thus be exposed to a number of different environments. This fluctuating correlation of the organisms and their environments can only with difficulty, and in exceptional cases, be controlled in free nature, while experiments with animals in captivity cannot always make up for observation in natural surroundings. It is, therefore, of prime importance to glance briefly at the experiences gained from the study of the growth of land plants, assuming while we do so that growth phenomena are of such general and fundamental significance that they must everywhere reveal important common features from which conclusions can be drawn for the understanding of marine organisms also. We will attempt such comparisons by considering the growth of the coniferous trees, the spruce and pine (*Picea excelsa* and *Pinus sylvestris*).

Every forester is convinced that he can gain from the annual rings shown in a tree stump a great deal of information about the condition and growth of the tree, — its life-history. Thus, he can discover that particular historical events, such as felling for the purpose of thinning out the trees in a "densely populated" wood, or ditching in marshy ground where the trees were stagnating, have caused radical changes in the growth of the trees. This ancient lore was greatly enriched, as we well know, by the new and exhaustive investigations carried out in forestry during the last generation. Most famous are the American studies of the gigantic trees known as *Sequoia gigantea* in California, and the whole of the historical research which used the ring system of the trunks for the registration or dating of historical events.

For us, however, the following results of the Swedish investigations into the growth, at various seasons of the year, of spruce and pine trees are of most interest. Romell, the Swedish forester, found that the top shoot (la pousse terminale intacte d'un nombre de jeunes arbres marqués) showed a brief seasonal growth, commencing as a rule in May and ending in the course of 2—3 months. During this period the top shoot grows in a manner which can be illustrated by a characteristic sigmoid curve. The course of this growth, as regards time, is remarkably akin to that found by fishery research from a study of the scales of herring and species of cod in Norwegian coastal waters. The growth shows a close correlation with the temperature. It begins earlier in southern than in northern habitats of the pine, and in the case of this species it was possible to establish a progressive movement from south to north in the Swedish districts in which it was studied. The growth of the spruce tree, on the other hand, proved to be so dependent on local surroundings that the influence of the climate in the direction of north to south could not be established.

In another series of investigations Langlet has studied the correlation of growth with the chemical changes. He found, as a universal rule, that the water content falls in the autumn or, in other words, that the dry substance then increases. At the same time the tree's store of starch declines, also its acidity and often the volume of chlorophyll, while sugar, fat substances, reserve cellulose, tannins and catalase increase. These changes, which seem to occur simultaneously and in conjunction with each other, are signs of the passing of the plants into the winter resting stage, that is to say, an onset of hardening in the tree.

When these events were studied by comparing the trees in different latitudes from north to south in Sweden it proved that in the northern areas the trees held more dry substances — sugar — substances which are extracted by petroleum ether and catalase. The dry substance thus discloses the physiological variability of the plants, and it was possible in the course of these investigations to reveal a continuous variation in the pine in respect of these physiological characters. In tests involving transplantation of the pine from northern to southern areas it was possible to establish, in some cases, that the content of dry substance was hereditary.

We can hardly fail to notice the harmony between the experiences from forestry and the investigations and problems which in recent years have preoccupied international co-operation for the

of the sea. And this comparison with forestry d that significance for marine research that lief in the influence of the environment on phenomena is strengthened by experiences have not encountered the same difficulties as which arise in connexion with the study of sms in the sea. In all studies of the growth the greatest difficulty is perhaps that which be found in the fact that, during their ions, the fish change their environment e are unable to follow their movements . Nor, in marine biology, are we able mentally to change the environment of the ls as forestry can do in the case of trees, can be transplanted from one habitat to r. In the papers by Einar Lea and Per stad which follow this paper of mine a r of illuminating examples will be found of ny problems which have confronted the study rine growth, and which have undoubtedly uted so much towards a widespread feeling is branch of study is beset with overwhelming lties.

is understandable, therefore, that the history studies of growth in reality denotes a series mpts to overcome these difficulties, and that ttempts have, in actual fact, consciously or ciously, been constrained to pursue the d we have referred to, of making a selection among the many events in nature in order to at a simplification of the problems, whereby, en cases, it must be assumed that large of factors are of no importance, while an dual factor can be proved to control definite s in growth from locality to locality.

we compare, from these points of view, the s geographical areas within the waters in international co-operation is effected we shall e that, *inter se*, they are separated from each n such a manner that both natural conditions, sheries from area to area, exert a different nce on the growth phenomena. In individual such as the southern part of the North Sea, hery — the catch — plays a much greater han in any of the other areas. In the rnmost areas, and especially in the North- n Area, the growth of the fish, at least o, has been comparatively independent of intervention in nature and has been deter- by natural conditions in the *milieu*.

e consciousness that human activity in the Eastern Area must be considered as a restric- ctor of the second order for the fish, in any s regards the growth of important species, s origin in the discovery that the fluc- ions in the age composition of the Nor- herring and cod populations, from one year ther, far surpassed, in quantitative respects, fect which fishing could be proved to exert. The growth phenomena are thus, as a matter of course, alternations between the organism and the external *milieu*, but the difficulty of proving this lies, as pointed out, in the movements of the organisms, the fish, across great areas of sea, within which variations in important conditions of life occur, such as temperature, salinity, and abundance of animals on which the fish subsist. Fishery research has, therefore, been constrained to enlist all available means of elucidating the life history of the fish in order to arrive, in each case, at the comparison between the biological phenomena and the particular *milieu*. The following brief references to the literature are given to illustrate how this has been done.

1. In the two first years of its life the **herring** is assumed to have a local habitat, and as there are young herring along the whole of the Norwegian coast it has been possible to compare the growth of these young herring in the various parts of the coastal waters. Lea has proved that the growth of the herring in the coastal waters of southern Norway takes place during the period April to September, while it stagnates between October and March. The optimum growth-rate occurs in May—June. Ottestad has compared the growth of herrings in their second summer from the south-west with that of the same group from north Norway and found a marked correlation with the sea surface temperature of these areas. In the southern area he found the same results as those of Lea. In the northern area the growth seems to cease as early as the latter half of August. These results remind us very strongly of the Swedish investigations of the top growth of young fir-trees in the Swedish forests at different latitudes. The growth must be considered as a series of growth-cycles of different duration according to the factors of past and present environments, varying therefore in the species, populations and individuals.

2. Lea has made the interesting observation that the scales of the young herring from north Norway have rings which are sharply defined, whilst herring from the southern part of the west coast have scales with more vaguely defined rings, and he has termed these two different scale-types "northern" and "southern". Runnstrøm has carefully studied a large material to test this statement and "agrees with Lea as to the correctness of his view" and he claims that it is therefore possible, by the study of the scales of older herring, to discover their growth-history in relation to the different environments which the species have visited in past years. By this means it was hoped to make a rational analysis and discover the connexion conformable to law between growth-rate and particular factors in the surrounding world. We are indebted to Lea, Ottestad and Runnstrøm for their interesting contributions to the solution of the difficult and complicated problem of whether the varying growth which is noticeable

on the coast of Norway is due to gradual changes in natural conditions, particularly temperature; or if it is rooted in more permanent types of growth which are comparable with the conceptions of hereditary races which have played such a great part, especially in the studies of the herring tribes. It is agreed that the spawning shoals are composed of growth-types from the different areas of the coastal waters. Thus, these growth-types do not live separately from each other, at any rate not all the time, as they are found to be mingled together when they are on the spawning grounds. Another feature common to all growth-types in the Norwegian coastal waters is that there is also a perfectly parallel fluctuation in the year-classes. The particularly abundant 1904 year-class thus greatly dominated the whole of the Norwegian herring population.

3. On the other hand, the exhaustive analysis of herring samples collected from many different parts of the Norwegian Sea indicates a great variation in conditions of life, which expresses itself in a corresponding difference in growth. Thus the fjords, the coastal waters proper, the open (oceanic) sea, the winter's spawning grounds, are all different, and they constitute, therefore, a series of environments which denote a great influence on the growth of the organisms. In the study of the characteristic difference of the winter rings in the different areas, and by the measurement of the breadth of the growth-zones on the herring scales attempts have been made to reconstruct the connexion between the history of the migrations of the herring and that of their growth.

Of the highest interest are the essays made by Lea to prove the migration of the coast herring to "oceanic" stages at various ages, some at the age of 1½ to 2½ years, others of 4½ or 5½, all according to the size attained at these ages. In the investigations carried out by Lea and Runnstrøm it has also been possible to extend this analysis to the spawning shoals. A peculiar "propagative" growth has been revealed and this has enabled them to establish that the spawning or "migration to the spawning shoals" begins at different ages, in individual cases at 3 or 4 years, in others at 5 to 6 and even up to 8 years. In these investigations we have a very much more varied or complicated picture of the events in the life history of the herring and their effects on its growth history than the first investigations in the North-Eastern Area disclosed. But precisely this complication must be said to strengthen the more general conviction which, from the outset, was the guiding factor in the initiation of this line of study, namely, the belief in the indivisible connexion between growth and *milieu*.

In many respects these new observations call to mind that example most characteristic among all experiences of the revolutionary effect of a change of *milieu* on the growth, namely, the passage of the salmon from the river stages to the oceanic mode of life, or to that of the great lakes. These enormous changes in growth fully remind us of the pictures of growth which are revealed in the conifers when marshland is drained or a densely wooded area is thinned out by scientific forestry.

4. The desire to make such an analysis, previously undreamt of, of the changes in growth has, no doubt, instituted the researches undertaken in recent years with a view to a more critical valuation of the hypothesis which the pioneers of these growth studies assumed to be more or less a matter of course, namely, that there was a parallelism between the growth-zones of the herring scales and the growth of the herring itself. It is of great importance that this original assumption has now been subjected to such a searching examination as that of the two papers of Lea and Ottestad which follow this statement of mine. Even if the comparison is susceptible of correction, the points of view advanced in these papers will undoubtedly throw light on the remarkable accord or correlation, which can here be proved to exist, of the growth of the entire organism with that of the individual organs.

5. The fact that we have been able to carry our search for these analytical problems so deeply in the study of the growth of the herring populations in the Norwegian Sea is no doubt due to the circumstance that we are here confronted with organisms the growth of which, wholly or partly, is controlled mainly by natural conditions alone, while the influence of man must be assumed to be entirely negligible. The interesting question, however, has been raised as to whether fluctuations in the density of population, which are not due to human intervention but to changes in the *milieu* during the actual spawning period, and which find expression in the varying number of individuals within the year-classes, can be proved to exert any influence on the growth of the herring. It is held that this question can be answered by statistical proof that the richest and poorest year-classes have both shown the same growth in one and the same sphere of the coastal waters, and that both of them acquire another growth-type, different from the first, if they stay in another area. It is of the greatest value that this question has been raised for further investigation in the future. On a more thorough examination of the history of migration of the single individuals from one *milieu* to another the problem will perhaps prove to be even more complicated than originally appeared to be the case. But it is to be hoped that the greatly improved methods which have now been adopted will render it possible to answer the highly important question, can even the most abundant year-class of herring find such rich sources of nourishment in the North-Eastern

hat its growth history will show no sign of estrictive forces of the environment", to use pression created by Malthus?

Even if it should be held that growth of the population in the North-Eastern Area will to some extent to be dependent on the fluc-s in density of population which result from rying number of individuals in the year-, there is undoubtedly unanimity of opinion e catches of the fishermen do not cause any which can be presumed to exert any ce on the growth of the herring. The same ion was also held at the time these studies ulation were begun in the other great fishery h in the North-Eastern Area, namely, that l to the investigation of the population of "**skrei**". Everyone who can remember actual observations 30 or 40 years ago on this species at a length of 1½—2 metres, o has found reason for fixing the age of ish at 20—30 years, will have retained the at the cod fishery which had been carried centuries had not, even up to that date, d that feature of the cod tribe which has een called "accumulated", that is to say, a omparatively untouched by human fishing. is generally known, conditions in regard to in the North-Eastern Area since that time ndergone enormous changes. The intensity fisheries has not merely doubled but has, in bability, been multiplied many times. Under rcumstances it is naturally of the very greatest ance to Norwegian fishery research, and not international co-operation, to follow the phenomena of the Norwegian stock of cod, s regards the method by which the average the spawning fish is investigated and the of the younger year-classes.

ring the earliest investigations in the ian Sea, in 1900 and the years immediately ing, it was discovered that the small fry spring from the spawning of the cod on the banks are carried and scattered by the s over the whole great Barents Sea area. time there was only a coastal fishery for ng cod, principally in the Lofoten Islands, r the younger year-classes off the most ly coast of Norway, namely, Finmarken. ous quantities of quite young stages were re hidden away and withdrawn from human tion. This picture of the life history of the s changed very greatly during the past 10 or rs as a result of the operations of fleets of trawlers off the coast of north Norway, banks outside the Lofoten and Vesterålen, Murman coast and, finally, in the vicinity Island. I am indebted to Dr. Lundbeck best information I have regarding these hing grounds, which shows that the masses wning cod are now fished on the banks he north-west coast of Norway, and that precisely those banks on which the youngest year-classes of cod grow up are those most intensively fished. Captain Thor Iversen has proved by means of a fine-meshed trawl that the number of cod in the catches on the banks south of Bear Island may consist of no less than 90 % of fish from one to two years old, which are thrown overboard by the trawlers as valueless. Experiences such as this have contributed greatly to an increased interest in the study of the growth history of the cod. Moreover, they have supported the efforts made for many years by the International Council to arrive at an international fishery convention, which was finally reached in March 1937 and which provides for a minimum mesh of 10·5 cm. for trawling in these northern waters.

From the somewhat incomplete statistics of the fishery in these waters it would appear that the draft upon the stock of cod has increased by several times its size in recent years. I consider, therefore, that it is my duty to take this opportunity to draw the attention of the Council to the important problems which this matter of the age composition of the stock of fish and its fluctuation from year to year must present to all countries which now participate in this fishery. Of equal importance are the growth problems as a means of evaluating the recent changes in the stock resulting from the increased fishery. In this connexion great significance must be attached to the information given by Gunnar Rollefsen in his paper, accompanying this report, from which it will be seen that, in his opinion, there are distinct signs in recent years of a decline in the average age of the spawning "skrei" during the great Lofoten fishery. From Oscar Sund's interesting marking experiments with spawning fish caught off Lofoten on the banks worked by the trawlers it emerges that both fisheries, the trawl fishery off the coast, and the line fishery in the coastal waters proper, take toll of the same stock. The problem, therefore, is, in a high degree, one of international importance.

For the studies of growth, moreover, it is of great interest that the investigations of the younger year-classes of cod, which are caught north of the coasts of Finmark, reveal a distinctly increased growth, which may possibly be explained by the assumption that the fishery has now reached a magnitude at which it reduces the density of population of these fish. This, therefore, must also be taken as a warning that there is indeed a great need for thorough investigation of the biological conditions of life for the economically important stocks of fish.

From the North-Eastern Area there are earlier experiences of changes in a stock of fish — an untouched or accumulated stock — namely, **plaice.** Bjerkan has observed old individuals which could be proved to have reached the age of 31 years. Where a stock of this kind has been fished

these old fish have inevitably disappeared and changes in growth conditions have become apparent in the younger year-classes. It is to be hoped that further information in regard to this may be forthcoming, as was the case in respect of the early years of trawling far to the east in the Barents Sea on the banks of Cape Kanin.

With these new events the North-Eastern Area is confronted by the same problems and its fisheries by the same troubles as those which for several decades have played such a great part in the fishing industry and in fishery research in the southern parts of the North Sea.

Bibliography.

1. Dahl, Knut: The Age and Growth of Salmon and Trout in Norway. London, 1910.
2. Hjort, Johan: Fluctuations in the Great Fisheries of Northern Europe. Rapp. et Proc.-Verb., Vol. XX, 1914.
3. Hjort, Johan and Lea, Einar: Report on the International Herring-Investigations during the year 1910. Publ. de Circ., No. 61, 1911.
4. Iversen, Thor: Nogen Iakttagelser over fiskeyngel i trålfangster i Barentshavet. Rep. Norw. Fish. and Mar. Invest., Vol. IV, No. 5, 1933.
5. Iversen, Thor: Some Observations on Cod in Northern Waters. Rep. Norw. Fish. and Mar. Invest., Vol. IV, No. 8, 1934.
6. Langlet, Olof: Studien über die physiologische Variabilität der Kiefer und deren Zusammenhang mit dem Klima. Meddel. Statens Skogsförsöksanstalt, H. 29, No. 4, Stockholm, 1936.
7. Lea, Einar: A Study on the Growth of Herrings. Publ. de Circ., No. 61, 1911.
8. Ottestad, Per: Statistical Analysis of the Norwegian Herring Population. Rapp. et Proc.-Verb., Vol. LXXXVIII, 1934.
9. Rollefsen, Gunnar: The Otoliths of the Cod. Fiskeridirektoratets Skr., 1933.
10. Rollefsen, Gunnar: The Spawning Zone in Cod Otoliths and Prognosis of Stock. Fiskeridirektoratets Skr., 1935.
11. Romell, Lars-Gunnar: Recherches sur la marque de l'accroissement chez le pin et l'épicéa durant la période de végétation. Meddel. Statens Skogsförsöksanstalt. H. 22, No. 2, Stockholm, 1927.
12. Runnstrøm, Sven: A Study of the Life History and Migrations of the Norwegian Spring-Herring. Fiskeridirektoratets Skr., Bergen, 1936.
13. Sund, Oscar: Merkning av torsk. Årsberetning vedk. Norges Fiskerier, Nr. 2, 1937.

2

NOTES ON STATISTICAL METHODS OF GROWTH STUDIES.

BY

PER OTTESTAD.

A. The problem of the growth of populations was most generally considered and discussed by Malthus and it was he who devised the growth function

$$y = m \cdot a^t \qquad (1)$$

in which y represents the size of the population at the time denoted by t. This formula can be accepted as a logically correct expression of the growth of a population under free conditions, that is to say, conditions in which there are no restrictive factors influencing the course of the growth.

B. The formula, however, does not correctly express the growth which we observe in nature or as a result of experiments. The rule in such cases is that the growth follows a sigmoid course. The growth increments are small at first but rise to a maximum, and then fall to zero. A number of attempts have been made to find a mathematical function capable of expressing this sigmoid growth in a concise manner. The most interesting formula which has been evolved is

$$y = \frac{b \cdot e^{at}}{1 + c \cdot e^{at}} \qquad (2)$$

which is based on the analogy of chemical processes, autocatalysis being regarded as a specific example of the mass law. In this connexion, however, it has been argued that this function is an expression of the results of the underlying biological processes. To this it may be said that the number of factors which determine the course of growth is so great and their mutual correlation and influence so complicated that, until more is known about these underlying biological processes, it is not practicable to seek for logical sigmoid growth functions. The immediate problem is that of finding a function which can serve to define the sigmoid growth with sufficient accuracy. If formula (2) is regarded from this angle the only objection which can be raised to it is that it is not a suitable instrument.

In a previous paper[1]) I have suggested that the construction of a theoretical curve should be founded on the growth increments rather than on the total growth. I demonstrated that in cases of symmetrical growth the increments can be described by the Gaussian frequency function

$$f(t) = \int_{t-\Delta t}^{t+\Delta t} \frac{1}{\sqrt{2\pi}\,\sigma} e^{-\frac{(t-m)^2}{2\sigma^2}} \qquad (3)$$

It will be seen that there are only two constants (m and σ) to be calculated in the actual case, and these constants measure the two most interesting parameters of the growth. m is a parameter which indicates the point of time at which the growth-rate attains the optimum value and 6σ is a measure of the span of time from the inception of growth to its fulfilment.

When the necessary observations of a growth line have been made and it is desired to describe this growth by the Gaussian function (3) the method of procedure is as follows:—

1. From these growth observations, which can be illustrated by an empiric sigmoid curve, the growth increments in the given time intervals are calculated. The growth increments are now regarded as the frequencies in a distribution series in which the time is the variable quantity. In Table 1[2]) particulars of the observations of the growth of a yeast cell population are given, and in the same table the growth increments are indicated.

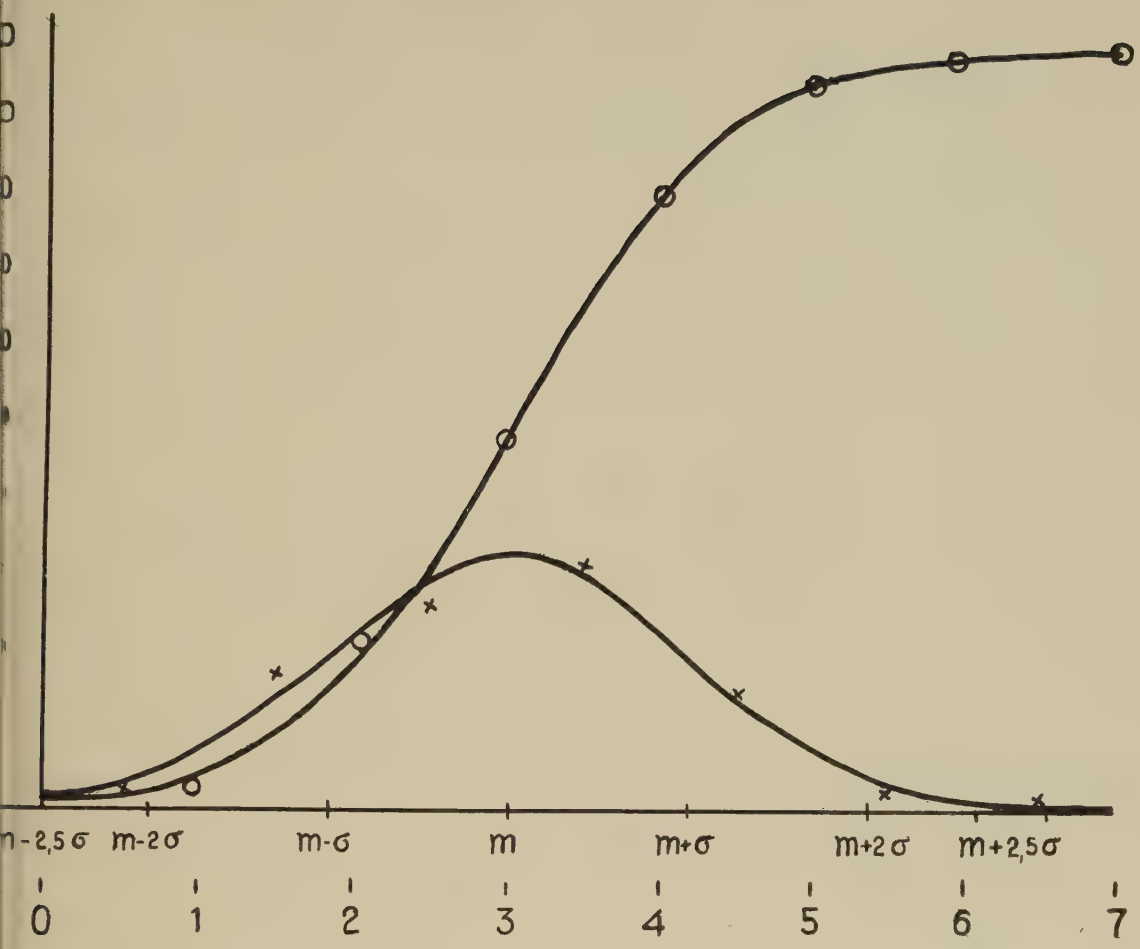
Table 1.

The number of yeast cells in 1/250 mm³., reduced to an assymptote of 100.

t in 10 hr.	Number of cells	Time-interval	Mid-point in interval	Increment $h(t)$
0	1·1	0—1	0·5	2·9
1	4	1—2	1·5	18
2	22	2—3	2·5	27
3	49	3—4	3·5	32
4	81	4—5	4·5	15
5	96	5—6	5·5	3
6	99	6—7	6·5	1
7	100			

[1]) Per Ottestad: A Mathematical Method for the Study of Growth. Hvalrådets Skr., No. 7. Oslo, 1933.

[2]) Oscar W. Richards: The Growth of the Yeast Saccaromycus cerevisiae. Annals of Botany, Vol. XLII, No. CLXV, 1928.



om such a frequency distribution the arith- mean (m) and the standard deviation (σ) w calculated in the usual manner. As regards tual method of calculating these two para- in practice almost any text-book of stati- may be consulted. The calculation of m for the distribution series in our example wn in Table 2:—

Table 2.
Calculation of m and σ.

t	$h(t)$	$t' = t - 2{\cdot}5$	$h(t) \cdot t'$	$h(t) \cdot t'^2$
0·5	2·9	—2	— 5·8	11·6
1·5	18	—1	—18	18
2·5	27	0	0	0
3·5	32	+1	+32	32
4·5	15	+2	+30	60
5·5	3	+3	+ 9	27
6·5	1	+4	+ 4	16
	98·9		+51·2	164·6

ee for example: G. Udny Yule: An Introduction Theory of Statistics. p. 133, London, 1929.

$$m = 2{\cdot}5 + \frac{51{\cdot}2}{98{\cdot}9} = 3{\cdot}0177$$

$$\sigma^2 = \frac{164{\cdot}6}{98{\cdot}9} - \left(\frac{51{\cdot}2}{98{\cdot}9}\right)^2 = 1{\cdot}3963$$

$$\sigma = 1{\cdot}18$$

3. m and σ now being known the values of the Gaussian function (3) corresponding to $h(t)$ can be calculated. I do not propose to deal with the different methods by which these calculations can be made. The method employed in the present case has been described in a previous paper[4]).

In the accompanying figure the values of the Gaussian function are compared graphically with the empiric growth increments. By simple summation the total growth can now be calculated from these theoretical growth increments. The theoretical growth-curve is entered in the same figure in which

[4]) Per Ottestad: The Exponential Frequency Function and Frequency Distribution. Metron, Vol. XIII, No. 1, Roma, 1937.

the original empiric growth-data are also included for the purpose of comparison.

The difference between formula (2) and formula (3) is not that one of them is more logical than the other, but that formula (3) is undoubtedly a more suitable technical instrument than formula (2). The technical advantage of using formula (3) becomes apparent when the problem is that of studying the influence which a certain factor exerts upon the growth, for instance, when two or more growth-curves are to be compared.

Both formula (2) and formula (3) can only be used in cases of symmetrical growth. If the growth is not symmetrical, however, we can use a skew frequency function as a description of the growth increments.

C. In a great number of cases the question is one of comparing the growth-rate in various parts of the same population growth-curve. If observations of the growth increments can be produced for every short span of time over the whole range of growth, it may be practicable to evolve a mathematical function which can serve as a description of the growth. In many cases, however, it is difficult to provide such observations, and where this is so mathematical functions may lead us astray. It is, however, more useful, and also more simple, to treat the observations statistically and the task thus becomes one of finding statistics by which the growth can best be described. These statistics are always conventional but among those which are applicable there is one method which, in the present case, is preferable to the others. It is necessary, however, to distinguish between

1. absolute growth increment, and
2. relative growth increment.

Both measures must be referred to a constant interval of time (Δt). The absolute growth increment is merely the difference between the size of the population (in weight or number) at the time $(t+\Delta t)$ and the size at the time t. If the size at the time $(t+\Delta t)$ is $y\ (t+\Delta t)$ and the size at the time t is $y(t)$, the absolute growth increment is

$$z = y\,(t+\Delta t) - y\,(t)$$

The relative growth increment may be measured in various ways, for example,

$$g \qquad \frac{y\,(t+\Delta t) - y\,(t)}{y\,(t)} \qquad \text{(a)}$$

$$g \qquad \frac{y\,(t+\Delta t) \quad y\,(t)}{\frac{1}{2}\,[y\,(t+\Delta t) + y\,(t)]} \qquad \text{(b)}$$

c) Another measure which has frequently been used is

$$g = ln\,y\,(t+\Delta t) - ln\,y\,(t) \qquad \text{(c)}$$

This formula has been derived from the formula

$$C_2 \quad C_1 \cdot e^g$$

where C_1 represents the capital invested at the beginning of a period and g the rate of interest. The formula is based on the assumption that g is a constant during the period of investment. The capital considered as a function of time is an exponential function. In the majority of biological cases, however, the "capital" function of time follows a more or less regular sigmoid course. My opinion, therefore, is that in most cases formulae (a) or (b) are more suitable than formula (c).

There is no doubt that formula (c) gives excellent and useful expression to the relative growth-rate in those cases in which the course of growth conforms to a certain type. Formulae (a) and (b) are nothing more than statistical recording instruments and they contain no assumptions in regard to the type of growth. It is quite immaterial which of them is used, the choice being a matter of personal predilection. General agreement, however, as to the formula to be used for describing kindred types of growth would be convenient and obviate misunderstanding of these technical terms or conceptions. But the choice of a formula must, naturally, also be determined for the particular problem in each case and the material at disposal. It is, however, most expedient that, in each case the formula used should be definitely stated.

In spite of the fact that formula (c) is restricted by certain assumptions as to growth it will nevertheless prove, in many cases, to be a useful one. It must be borne in mind, however, that a definite relation can be set up between formula (a) and formula (c). If the relative growth-rate measured by formula (a) is represented by g_a and measured by formula (c) it is represented by g_c. The following equation can be stated:—

$$g_c = g_a - \frac{g_a^{\,2}}{2} + \frac{g_a^{\,3}}{3} - \frac{g_a^{\,4}}{4} + \cdots$$

It will be seen from this that when g_a is small, that is to say, the growth is small, g_c and g_a will be very nearly equally large, and will express one and the same thing. In such cases it is perfectly justifiable to employ formula (c) as a measure for the relative growth-rate.

3

A MODIFICATION OF THE FORMULA FOR CALCULATION OF THE GROWTH OF HERRING.

BY

EINAR LEA.

THE growth of an organism is a fundamental part of its life. It is therefore justifiable to assume that, where they are available, descriptions of growth history will be of significance. This does not apply merely to investigations in which growth occupies a prominent place, but also to those in which, although the problem does not directly involve the growth of the organism, the phenomena under consideration are, nevertheless, dependent in one way or another on growth. To mention one or two examples only, it can now be seen that it would have been of material help if growth-data had been at the disposal of H e i n c k e and his successors in the biometric line of work, and that the study of the ramifications of the influence of the sexual functions on the life history of fish, *inter alia*, on their migrations, is rendered more difficult or facilitated all according to whether information on growth is, or is not, available.

From considerations of this nature it must present itself *per se* as a useful and important task to develop methods for individual growth determination in those cases in which this is possible. A possibility of this kind exists in the case of the herring and probably also of those species of fish in which the annual rings on the scales or bones are sufficiently definite to permit of fairly precise measurements being taken.

The conception that the permanent picture of the growth of the herring scales, which is registered by the formation of annual rings, can be employed for calculation of the individual growth of the fish expressed in the conventional measure — the total length — has its origin, to some extent, in a number of more or less precise observations which are brought forcibly to the notice of everyone who performs the basic observational work on actual herring samples and does not start the work from tabulated observations made by others. To some extent the conception arises from more precise observations of the arrangement of the annual rings on the scales.

Irrespective of whether he examines his herring samples biometrically or otherwise an observer cannot avoid noticing such matters as that fish varying greatly in size have, nevertheless, in their broad features approximately the same shape; that the number of scales and their arrangement on the body are, on the whole, the same; that scales which have a definite situation and a characteristic form occur at the same place and with approximately the same form in both small and large fish; and that the size of the fore part of the scales, that which has a fluted surface, corresponds to the width of the muscle segment which the scale overlies and covers.

Observations of this kind naturally give birth to the idea that in its development from a small to a large fish the herring acts approximately as an isomorphous body or, to use H u x l e y's terminology, the herring has an isogonic growth. In this connexion it is of interest to mention that in his work "Problems of Relative Growth" (1932), which is mainly devoted to organisms and organs with conspicuously heterogonic growth, H u x l e y cites ichthyometric data as an illustration of isogonic growth.

The simple proportion formula for growth calculation,

$$l = \frac{s}{S} L,$$

is none other than a precise mathematical formulation of this conception of isomorphous growth in so far as concerns the quantities used in the formula, and it is more or less valid in the same measure as the conception corresponds more or less exactly to the actual conditions.

Simultaneously with this conception, certain critical counter ideas also arise from general observations of this nature. To a fairly well-trained observer it is sufficiently obvious merely on inspection and comparison of samples of both small and large herring that the form of the individuals irrespective of size is not exactly the same. There is undoubtedly a small but nevertheless obvious difference in the bodily proportions between the large and the small individuals, and this difference proceeds in a definite direction; for example, the head of the small herring appears comparatively larger than that of the large herring.

omorphism (or isogonism) cannot therefore plete and the proportion formula mentioned cannot be expected to give an absolutely expression of the actual conditions.

more precise observations, which operate in ie direction to stimulate the idea of exploiting wth history registered on the scales, concern rrangement of the annual rings ales from the same individual. rrangement, to which numerical expression sily be given by measuring the distances ne growth-centre of the scale to the winter s well as the scale-edge, and converting all ements into units or percentages of the last ment, shows such great similarities when the n is one of measurements from adjacent even if the absolute measurements of the happen to be conspicuously dissimilar and gular changes in the numerical values where eries of scales are concerned that it is im- ly necessary to seek an explanation. In my , this conformity to rule is incomprehensible the facts observed are supplemented by the tion that the observable growth ries which the scales reveal ry closely allied to the growth e individual as a whole, and thus the increase in the measurement which is ionally used to indicate the size of the ual — the total length.

ervations of this kind, which can also be d to several measurement dimensions of the ale and even to characteristic details of the on of the winter rings (sharp or diffuse louble ring formations and the like), form, pinion, the real basis of, and argument for, nviction that the actually existent and able growth history of the herring scales converted into expressions which are compar- th the conventional measurements of length rical lengths").

acceptance of this close connexion between ich, for the sake of convenience, we may e growth in length of the herring and the special growth histories, which can be d directly on the bones and scales, is dent of, and thus also compatible with, onception of how the connexion can best nulated in a mathematical equation applic- a definite measurement dimension of a ar scale. It is *per se* possible that the in certain definitely localized scales really ic ently isomorphous with the growth in ir which case the already mentioned simple ion formula is valid for these scales, and it ible that the connexion for other scales tely other scale dimensions) can best be d by other mathematical equations. To e this is an important technical or practical the development of the growth method, and conceivably be done in several ways. But the result of this work cannot be at variance with, nor change anything in, the above-mentioned similarities (or regularities) with regard to the particular growth histories, which are revealed by a consideration of the annual ring system of the scales.

We can even, in principle, renounce, or save ourselves, the work of discovering an equation which connects the growth in length with the growth of a definite scale, namely, by defining the growth history of the individual as that which the scale reveals. We must then, it is true, at the same time abstain from using the length as a conventional expression of the size of the individual, and use instead the size of the scale to express it. Strong objections of a practical nature can be raised to such a change in the conventions, e.g., that a scale is such a small element of the organism, or that it will make it difficult to define the size of individuals which have not yet acquired scales, and so on. But, in principle, as far as I can see, there can be no objection to adopting this line of thought; and, in fact, practical application of this solution has been given effect in a work by E. M. Watkin (1925).

The conviction of the intimate connexion between the thousandfold particular growth pictures, which are registered on the scales of a herring, and the growth of the individual as a whole is thus founded on facts which can be observed in the one individual alone and in repetitions of this class of observations individual by individual. It is not founded on results which are acquired by a collective analysis of samples of herring. It is a different matter that in the course of the work of drawing up calculation formulae it has been found necessary to operate with such collective data. The necessity for this is not a matter of principle but is due to the fact that it has not been technically possible, in any event as far as the herring is concerned, to follow the connexion by means of individual observations. In the case of other species of fish such individual observations may feasibly be carried out in aquarium experiments, as performed by Thompson (1926), and specially arranged marking experiments. Ø. Winge (1915) has succeeded in obtaining a few individual observations of this kind by marking cod.

In the practical-methodical work of developing formulae for the calculation of growth, and in the critical investigations which have been carried out different methods of procedure have been adopted. (As the use of the simple proportion formula has been extended to many species of fish, and as both methodical work as well as valuating views are contained in works on fish other than the herring I refer to some of these in the following remarks).

In one group of investigations represented by K. Dahl's work (1910) on salmon and trout, Rosa M. Lee's (1912) on herring, salmon, trout

and haddock, and many others, the statistical tests are intended to decide whether the growth figures which are obtained by the employment of the simple proportion equation are plausible, that is to say, whether they answer to what is considered legitimate expectation. In this class of investigation average values have been chosen for "empirical" length measurements to act as prototypes, and the extent of agreement between these "empirical" average values and the corresponding "calculated" average values has been regarded as expressing the degree of "correctness" of the latter.

A variant of this type of investigation is found in Rosa M. Lee's work (1912) in so far as, in addition to the comparison mentioned, she also uses comparisons between corresponding calculated growth figures for different age-groups. It is by means of this kind of calculation she arrives at what she has termed "the apparent decrease in growth-rate with increasing age", that is to say, the fact that the growth figures for the older animals in a sample generally have, on an average, lower values than the corresponding figures for the younger animals in the samples; and it is mainly on this circumstance that she finds grounds for holding that the growth calculation method cannot yield correct results. C. Segerstråle (1921) has, so to speak, systematized this idea by searching for measurement dimensions on the scales, which, by the use of the simple proportion formula, lead to calculated values with the greatest possible accord with the "empirical" average.

In another form a similar method for testing is taken as a basis in Hodgsons (1929) work. Instead of comparing corresponding average values of calculated lengths for different age-groups (of different year-classes) he compares corresponding length-frequency curves for the same year-class in catches from different years. And as, in his data, these curves have a comparatively characteristic, multimodal form, more and better evidence is provided in the comparison for a critical test than in a comparison of arithmetic means.

Possibly this kind of criterion may be considered as having a certain degree of importance in cases where it is a question of investigating whether the calculated growth figures are fairly correct. But it is clear that great uncertainty attaches to this procedure. It assumes, in effect, a knowledge that the average values of the calculated growth figures must actually agree with the corresponding "empirical" average figures in order to be correct; and in what concrete cases can such an assumption be upheld with certainty? Moreover, the question of what can be regarded as a satisfactory accordance will here, as elsewhere, depend on the requirements of the various problems.

In another group of critical investigations the nature of the calculated growth figures, whether they appear to be plausible or otherwise, has been entirely disregarded, and attempts have been made (a) either to find independent criteria for discussing the legitimacy of the simple proportion formula, or (b) on the basis of such independent criteria to construct other equations for calculating growth. To the first sub-group (a) belongs my work of 1910 and Buchanan-Wollaston's (1934), to mention two extreme points in time. To the other sub-group (b) belong such works as those of Rosa M. Lee (1920), Huntsman (1918), Graham (1929), for cod, and a number of others.

In all investigations within this group use has been made of collective data, but in some cases in very different ways, and in all of them occurs the size S (= a linear dimension as a measure for the total length of the fish). In the majority of the works under sub-group (b) use has also been made of the technique of the correlation theory, either in its more primitive empirical form (e.g., as in Huntsman where S is plotted against L in a co-ordinate system, and a line drawn as nearly as possible to the L—S points), or with the application of the formulae of the theory for the calculation of the correlation co-officiant r and regression lines.

A number of these works (Meek 1916, Rosa M. Lee 1920) also take into account the fact that the scale covering is not formed until the herring are 3—5 cm. long, and it has been asserted that a formula such as the simple proportion equation

$$l = \frac{s}{S} L$$

cannot be valid for this reason, as it of course describes straight lines which all start from the origin.

When we try to decide whether the technical-methodic investigations hitherto carried out have resulted in a clear understanding of the validity of the growth methods, I think that this is not the case. And this applies irrespective of whether we enquire if the simple proportion equation has been more firmly established or whether some other well-founded formula has been advanced which yields results more in accord with reality.

Presumably it is unnecessary here to demonstrate this in detail, particularly in view of the fact that the opinions of the individual workers in regard to methods of growth-study differ so widely, some of them, such as Hodgson, taking the view that the original simple proportion formula is essentially sound whereas others are more reserved and some of them (Molander 1918) to all intents and purposes appear to consider that there is no rational basis for converting the growth history of the scales into terms of the total length.

This does not mean that the work hitherto done in connexion with the methods has been in vain, or that it is of no value. This is not the case since, *inter alia*, the work is of use in drawing up a

for new investigations for the establishment methods of growth-study.

must the conclusion be drawn from what en said above, that the great number of cal investigations which are carried out by of growth calculations are influenced by the ration. For in the majority of these, regard en had to the circumstance that the simple ion formula cannot in general yield al results which are entirely faithful to conditions. This was expressly emphasized ago as in my earliest work (Lea 1910, 2).

he foregoing is a fairly correct statement of e of affairs as they are at present it should, pinion, stimulate us to continued efforts to ie growth method on to a more secure basis. this motive another must be added, which ecial weight in connexion with investigations to herring in Norwegian waters. In regard herring the first point to emerge from all s investigations is that there is a great y in the size of the individuals within a year-class. This is undoubtedly a con- e of the differences in *milieu* over the wide distribution of this Norwegian herring. y, great differences are revealed between t year-classes, and this, presumably, is also d with the difference in the external con- under which the individuals of the various sses have grown up. These diversities, which rom an early age onward, can be traced the aid of growth calculations from the merely with the help of data referring to size.

a result of these differences the single als of a year-class have, to some extent, a varying history, as shown for example by that some of the individuals of a year- in the spawning shoals when they are not an 3 or 4 years old, whereas others wait ey are 5 or 6 years, or even 7 or 8 years; ne proportion in which a number of the als of the year-class terminate the coastal f life as young herring of $1\frac{1}{2}$ or $2\frac{1}{2}$ years s into an oceanic stage, while others post- s until they are $4\frac{1}{2}$ or $5\frac{1}{2}$ years or more. nilarly the result of the differences is that viduals of the different year-classes act ly in these respects. They are reflected the possibilities which present themselves ar to year of catches of young herring, and make their influence felt in the fishing for ar herring, in as much as, for example, a al le influx of fish spawning for the first n cause great changes both in the quality atches and in the course of the fishery.

an hardly be contested that the study of enomena must form a very important part orwegian herring investigations. Similarly cannot be denied that a sound method of calculating growth would be of prime importance in such investigations.

My opinion in this respect has been strengthened by reading Runnstrøm's (1936) paper on the Norwegian herring. In this the author has used growth-data obtained by means of the simple proportion equation from a material divided into groups according to the "character" of the winter rings, a systematization the principles of which I set forth in 1926—1928 (Lea 1929). In conformity with these principles it is possible to divide a sample of Norwegian herring into a large number of categories, (a) according to whether the individual herring has passed the first part of its youth in southern or northern coastal waters, (b) according to whether the coastal life has stretched over 1, 2, — 6 winter seasons, and (c) according to whether the subsequent oceanic young stage, during which sexual maturity is completed, has covered, 1, 2 or 3 winter seasons (more correctly, periods for the formation of winter rings).

The growth-curves which can be drawn up for the various categories have such characteristically different courses (see, for example, Fig. 9, page 77 of Runnstrøm's paper) that, as far as I am concerned, I cannot avoid drawing the conclusion that by combining the two methods of observation (sorting according to the scale character and growth calculation) many fresh possible ways are opened up for investigating several important processes which take place in the Norwegian herring population — the grouping of the young herring on the coast in shoals according to size of fish and the re-grouping among these; the passage from these shoals of the individuals entering the oceanic stage; the accession from this oceanic group to the spawning shoals. All these processes are closely concerned with the growth of the individual and their occurrence can be apprehended by the methods as they now stand. Nevertheless we may hope to describe them more precisely, and perhaps also to calculate them quantitatively, if the methods can be improved.

The disadvantage of using the simple proportion formula

$$l = \frac{s}{S} L$$

as an equation for calculating growth lies in its lack of a term which compensates for heteromorphous growth. In my first work I tried to effect such a compensation in two ways, (1) by setting up a compensation table, valid for the scales immediately behind the gill-cover, and (2) by seeking a part of the body where the scale grew as little as possible heteromorphously with the growth in length. In spite of the fact that the correction table mentioned in (1) still has, in my opinion, a certain value as regards the scales in question, it is readily admitted that it does not

fulfil the requirements to-day. And both methods of compensating cannot be said (in any event as far as Norwegian herring are concerned) to be practical. This is because, for determination of age, scales should be taken from the middle region of the 5th—12th muscle segment, and not from immediately behind the gill-cover or from the 25th—28th muscle segment as assumed by alternative (1) or (2). As there is a difference in growth between these three groups of scales, either it will be necessary to collect duplicate sets of scales, one for the age-census and one for the measurement of growth, a cumbersome method, or a new correction table must be drawn up applicable to the scales best suited to age determination. If it is decided to take this course, it must of course be done as efficiently as possible.

The disadvantage arising from the lack of a compensatory term in the calculation formula does not lie in a lower degree of precision in the observations, nor are the advantages of a suitable correction to be found in an increase in the precision, if by precision is understood the chance errors of the observations. The disadvantage arises from the fact that the observations show a systematic error, the numerical value of which is not constant but is dependent, *inter alia,* on the difference in size between the measured total length and the estimated length of the 1st, 2nd, etc., winter ring.

The result of this is a varying degree of comparability in the case of corresponding growth figures (e.g., l_1) from groups of different total lengths. In a carefully made analysis of a material this circumstance involves no small amount of work in ascertaining which observations are really sufficiently comparable for the purpose in question and which of them cannot be regarded as being so. Moreover, the material cannot be so fully utilized, because it is necessary to refrain from drawing comparisons which are desirable in themselves.

In other words, the use of the simple proportion formula is uneconomic, just as it would be uneconomic to use uncorrected thermometers for hydrographic surveys. Furthermore, satisfactory elimination of the systematic error previously mentioned will increase the number of permissible comparisons of growth-data in a given material and make the work easier and more certain. The procedure followed in my work for obtaining a better growth formula is described below.

The Material and Observations.

The basic observations used are the total length L as an expression of the size of the fish, and a linear dimension S to express the size of the scale, in agreement with previous practice. In my early work (1910), however, I chose a scale which was easy to find but which is not normally used in the ordinary routine collections and investigations, and a dimension for this which, from the point of view of the technique of measurement, was convenient for this particular scale but which is inconvenient when measuring other scales. In the subsequent collection of material I have selected a scale which is situated in the seventh horizontal scale series from the edge of the belly and which is No. 7 from the operculum. This scale was chosen for two reasons, (1) because it is situated in that region of the body of the herring where the age-rings on scales of old animals are easiest to discern, and (2) because there does not appear to be any noticeable difference in average size between this scale and its neighbours. This latter circumstance enables one to substitute one of the adjacent scales for the selected scale if this is missing or must be excluded from the material because it is regenerated or shows signs of mechanical dislocation. In the collection of material two neighbouring scales, Nos. 6 and 8, were included and used in particular cases.

The method of measurement which was used is the same as that employed in the routine work, the distance from the "growth-centre" to the edge of the scale along a line as perpendicular as possible to the somewhat uneven basal line between the fluted and smooth parts of the scale. The growth-centre of the majority of scales used can easily be localized by means of certain peculiarities in the scale surface immediately below the basal line, which has a characteristic bend there.

The material collected consists of samples of Norwegian herring of as many different ages and sizes as possible, from samples of herring of less than a year old to fully grown individuals of more than 15 years. They range over the entire area of growth measurements, from the formation of the first ring to those many years old.

Each sample has been kept separate and divided into sub-groups according to age.

Treatment of the Observations.

The first step in the treatment of the material is dictated by the following considerations:—

If in the case of a sub-sample of old animals, say, 15 years of age, the mean value $\overline{L}$ of the length and the mean value $\overline{S}$ of the size of the scale are taken as co-ordinates in a cartesian co-ordinate system, the point $(\overline{L}, \overline{S})$ will represent the terminus of a line, every point on which represents the mean values of $\overline{L}$ and $\overline{S}$ of the individuals of this group at previous periods in their life, and this applies irrespective of whether the individuals have been in company with each other the whole of the time or separated. The line is called the mean-point line for the group of individuals in question. It is not ascertainable from the observations under consideration. These, however, can supply a mean-point for each sub-group, and as these sub-groups cover widely differing ages

zes the material provides a collection of nt mean-points, each of them valid for its ›up in the material.

this collection of mean-points in the co-e system showed no regular order, it would ve been possible to do anything more with it so happens that the points are arranged a manner that a representative line can be between them. From this circumstance it concluded that these separate mean-points nt something general, which connects the ›ups investigated, and that the unknown oint lines for all sub-groups lie along this ntative line.

this case it is possible to determine all the alues of L in respect of the earlier periods life of a sub-group for which the mean f S can be established, and this can be done e times at which the winter rings were . We thus have a method for calculating rage size for groups of the above-mentioned ge-groups) on the formation of the 1st, 2nd, nter ring. This method is used below as an ry method.

question of how the series of mean-points t be represented as a line can be dealt with ral ways. The line can be drawn by eye, a assessment can be made, regard being had precision of the individual mean-points, or hmetical interpolation or graduation may ormed. In my own material the series of oints is grouped with sufficient regularity straight line, so that there are no grounds sidering any equation for the representative ner than

$$\overline{L} = a + b\overline{S} \qquad (1)$$

a similar treatment of the observations are to be found in the papers by Rosa e (1920) and Molander (1918), and lasting the observations in my paper of 1910, rrive at essentially similar results, in spite fact that these three collections are not comparable with my own later observations, e e's material cannot be split up into sub- according to age, and Molander's on of scales was not derived from a definite the body of the fish.

he assumption that equation (1) is available ulating the mean lengths $\overline{L}$ when the mean- $\overline{S}$ for sub-samples of animals of the same known, the further reasoning will be as —

a sufficiently large material of n older fish same age, the mean-point of which for the ngth and size of scales $(\overline{L}, \overline{S})$ lies on the line equation (1), measurements are also part from L and S of the distances between wth-centre and the 1st winter ring, and are . For each individual we have the three observations s, S and L, and to each set of this kind there attaches an unknown l, that is to say, the length which for the individual in question appertains to the s of the individual.

For the total of n individuals we have

$$\frac{\Sigma l}{n} = a + b\frac{\Sigma s}{n},$$

this equation being merely a transcription of equation (1).

For each single individual in the material we can state a strictly valid equation of the form

$$\frac{L - \alpha}{l - \alpha} = \frac{S}{s} \qquad (2)$$

This equation expresses nothing more than that a straight line can always be drawn between two points (L, S) and (l, s). As l is unknown in each individual case α cannot be assumed to be common to all individuals and must be furnished with an index in common with the unknown l and the known magnitudes s, S and L. Solving equation (2) for l we obtain

$$l = \frac{s}{S}L + \alpha\left(1 - \frac{s}{S}\right) \qquad (3)$$

In this equation, as will be seen, the first term to the right is identical with the calculated lengths obtained by the use of the simple proportion equation and this value is called below l'.

The second term is a correction on l', the magnitude of the correction depending on the unknown α and the known expression $1 - \frac{s}{S}$, the numerical value of which is equal to $1 - \frac{l'}{L}$ and is always a proper fraction.

For the complete sample the following equations can be stated:—

$$\begin{aligned} l_1 &= l'_1 + \alpha_1\left(1 - \frac{l'_1}{L_1}\right) \\ l_2 &= l'_2 + \alpha_2\left(1 - \frac{l'_2}{L_2}\right) \\ l_n &= l'_n + \alpha_n\left(1 - \frac{l'_n}{L_n}\right) \end{aligned} \qquad (4)$$

which on adding yields

$$\Sigma l = \Sigma l' + \Sigma\alpha\left(1 - \frac{l'}{L}\right). \qquad (5a)$$

Divided by n (the number of individuals) this produces

$$\overline{l} = \overline{l'} + \frac{1}{n}\Sigma\alpha\left(1 - \frac{l'}{L}\right) \qquad (5b)$$

If now, in the equations (4) instead of the individual quantity α we introduce a quantity A common to all individuals we obtain

$$l_1 = l'_1 + A\left(1 - \frac{l'_1}{L_1}\right)$$
$$l_2 = l'_2 + A\left(1 - \frac{l'_2}{L_2}\right) \qquad (6)$$
$$l_n = l'_n + A\left(1 - \frac{l'_n}{L_n}\right)$$

which on totalling gives

$$\Sigma l = \Sigma l' + A\Sigma\left(1 - \frac{l'}{L}\right). \qquad (7a)$$

this on division by n yields

$$\overline{l} = \overline{l'} + A\frac{\Sigma\left(1 - \frac{l'}{L}\right)}{n} \qquad (7b)$$

Comparing (5 b) and (7 b) it will be seen that the latter equation gives the same result as the first if

$$\frac{1}{n}\Sigma\alpha\left(1 - \frac{l'}{L}\right) = \frac{1}{n}A\Sigma\left(1 - \frac{l'}{L}\right) \qquad (8)$$

and as in (7 b) all quantities except A are known this equation serves to determine A.

It is thus possible to work out an equation of type (6) for individual calculation of the growth, which is of such a nature that it causes the mean values of the calculated growth figure to be equal to the mean values which are obtained by calculation according to equation (1). In this way, presumably, the systematic error in the simple proportion equation should be eliminated to an extent which depends only on the accuracy with which equation (1) can be established once and for all. This, in the main, is a question of the number of observations made with a given degree of accuracy.

The numerical value of A lies, according to the calculations so far made, between 8 and 12 mm., varying according to the assumptions upon which the quantity a in equation (1) is computed. On this point my work on the material is not complete and I therefore state the value of A as 10 mm. provisionally only, though I believe it to lie close to the true figure.

In the construction of this new growth equation the quantity A is not invested with any biological or morphogenetic significance and must by no means be connected with the apparently similar constant a which occurs, for example, in Lee's (1920) proposed growth formula. This quantity a, the numerical value of which is put at 30—40 mm., by Molander at 50 mm., represents the length of the herring immediately before the scales begin to grow out on the herring, and it is placed directly in the equation without any attempt being made to demonstrate that the

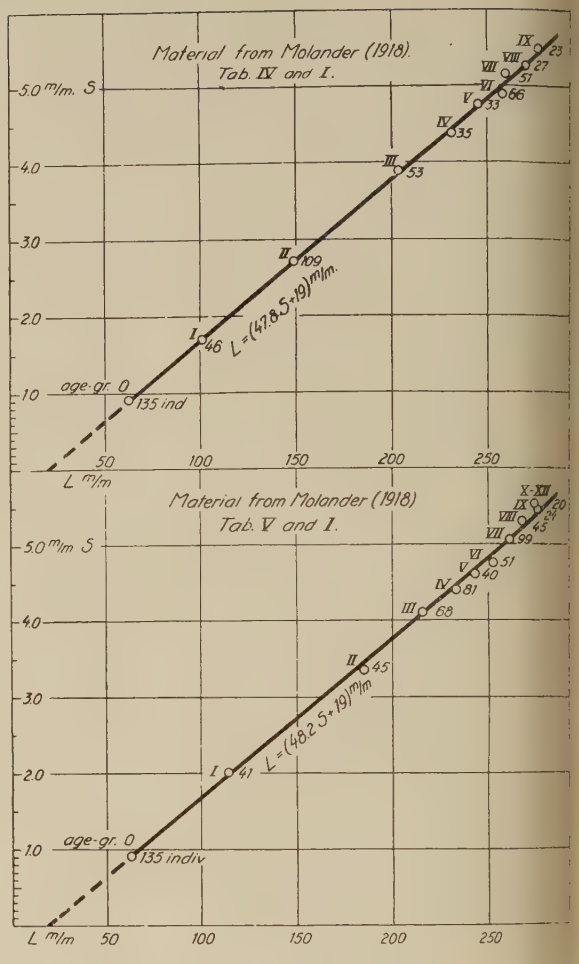


Fig. 1.

function line, which is being sought for, really runs straight from the point $s = 0$, $L = 30$—50 mm., which is a tacit assumption that $a = 30$—50 mm. can justifiably be introduced into the equation. It can be proved from Molander's own material that this assumption does not hold good, and it emerges both from this material and from my own observations that the function line (equation 1) which runs in a straight line in the area of the growth calculations (from the 1st winter ring and onward) also maintains this straight course for a while below this area. The position of Molander's observations in this respect is shown in Fig. 1, where they are used to determine the course of the mean-point line. In the uppermost section of the figure material from Molander's Table IV is used, in the lowest section material from his Table V. In these two tables are recorded the number of individuals in each size-group (cm.) within each age-group, and for each individual group the mean value of scale size is indicated in

m. It is therefore possible to find $\bar{L}$ and $\bar{S}$ ach age-group, and each table, consequently, lhes a number of mean-points.

otting these mean-points in a co-ordinate n shows that in the case of both samples the are arranged fairly obviously along a nt line represented by the equation $\bar{L} =$ + 19) mm. In estimating the validity of results the following information from a n d e r's commentary must be taken into nt:— (1) Three scales from each fish have measured. This will, to some extent, eliminate ntal variation in the scale size and thus be tageous; (2) The scales have been taken at m (3 scales, no matter which), that is to say, neasurements do not refer to definitely ed scales. This circumstance gives rise to s concerning the suitability of the data for ucting a mean-point line; (3) The measure- employed for S is the distance from the line to the edge of the scale perpendicularly e basal line. This measurement is slightly an that which I have used. The resulting nce exerts no influence on the constant *b* in on (1), but on the other hand the constant *a* ongly affected. A calculation shows that a nce of 0·2 mm. between M o l a n d e r's and measurements of S reduces the value of *a* o l a n d e r's material from about 20 mm. to 10 mm. In Norwegian herring the difference en the two measures is of the order of 0·13 and if the difference was of a similar order in a n d e r's scale material it implies a reduction o about 14 mm., thus bringing M o l a n d e r's sh and my Norwegian material into satis- y agreement, considering the amount and y of the material.

h e above also provides an nple of the way in which even a small difference in observa- al technique may cause appa- disharmony in the results and nphasizes the necessity for pre- definitions in work of this

ter the two mean-point lines had been shed a new mean-point was marked off which calculated from data in M o l a n d e r's I. This table is of great interest because it to a sample of very small herring from 53 mm. in length, with an average of 63 mm. a n d e r records certain observations which e that the herring in Swedish waters do not e scales until they are about 50 mm. long. ample in question, therefore, is only about . further advanced in length than the scale- erring. Nevertheless, the mean-point for this e is on exactly the same line as the mean- for the larger and older group (and this is he case in my material of a similar kind).

e validity of the straight mean-point line

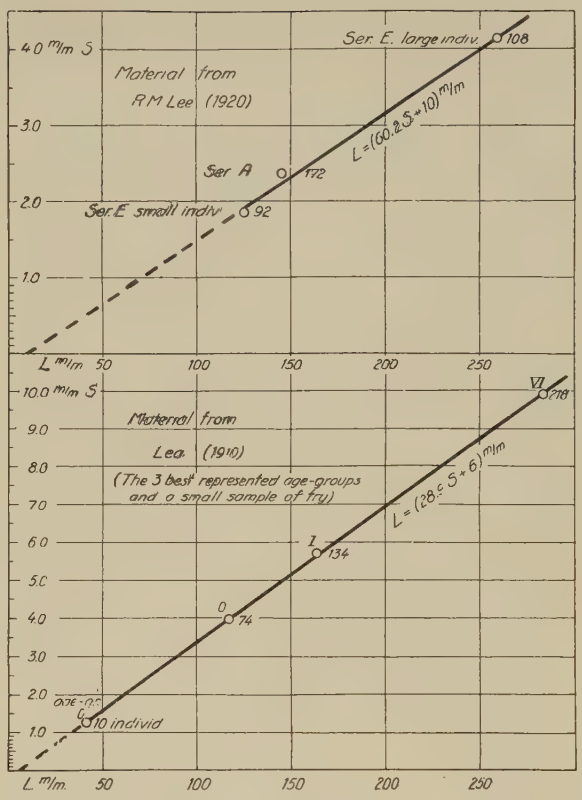


Fig. 2.

(equation) thus extends far down towards the length at which scales first appear on the herring, a circumstance of great importance for justifying the use of the growth equations. This finding also serves to show the untenability of all the views which have been advanced in connexion with the circumstance that the herring does not acquire scales before metamorphosis.

Fig. 2, uppermost section, shows the results of an analysis corresponding to the foregoing which has been carried out with the observations to be found in L e e's work (1920) and the lowest section is based upon data from L e a (1910) analysed in the same way. In L e e's work the individuals are not grouped according to age and no mean-points can therefore be calculated for age-groups. But as a part of the material (Table 2) forms two distinct size-groups and as in addition there is one more sample, 3 mean-points of a somewhat more complex significance can be calculated. It should be borne in mind when considering these mean-points that when two points (or more) lie on the same straight line, so also does the point, the co-ordinates of which are the mean values of the co-ordinates of the individual points; in other words, if the mean-points of the unknown age-groups in such compound groups lie on a straight

line this is also the case with the more complex mean-points which can be calculated from the material.

As will be seen from Fig. 2 the mean-points lie as well as can be expected on a straight line and the constant *a* has, for Lee's data, a value of about 10 mm., and is thus also of the same order of size as in the Norwegian and Swedish material (after correction for a difference in measurement). For Lea's material, which deals with the earshaped scale situated behind the gill-cover, the straight course of the mean-point line is very clearly indicated. The constant *a* is about 6 mm. long, whereas *b* has a value entirely distinct from that in Lee's and Molander's data, since both scale and measurement dimensions are quite different.

There should accordingly be reason to expect that it will be possible to arrive at a growth-formula for herring in which the effect of the heteromorphous growth in the two dimensions L and S is largely compensated. The conditions for the attainment of this goal are that adequate material is collected once and for all for as many herring populations as possible, and that this material is measured in the same way and dealt with by calculation according to the same principles.

Literature.

Buchanan-Wollaston, H. J. 1934. The Theory of Variation, Correlation and Regression. Its Relevance in Researches on Proportional Growth. Rapp. et Proc.-Verb., Vol. LXXXIX, Copenhagen.

Dahl, K. 1910. Alder og Vekst hos Laks og Ørret i Norge. Landbruksdept. Oslo, 1910. Engl. Edit. Salm. and Trout Assoc. London, 1911.

Graham, M. 1929. Studies of Age-Determination in Fish. Fishery Invest., Ser. II, Vol. XI, No. 2. London.

Hodgson, W. C., 1929. Investigations into the Age, Length and Maturity of the Herring of the Southern North Sea. Fishery Invest., Ser. II, Vol. XI, No. 7. London.

Huntsman, A. G. 1918. The Growth of the Scales in Fishes. Transact. Roy. Canad. Inst. Toronto.

Huxley, Julian S. 1932. Problems of Relative Growth. London.

Lea, E. 1910. On the Methods used in Herring Investigations. Publ. de Circ., No. 53. Copenhagen.

Lea, E. 1929. The Herring's Scale as a Certificate of Origin. Rapp. et Proc.-Verb., Vol. LIV. Copenhagen.

Lee, R. M. 1912. An Investigation into the Methods of Growth Determination in Fishes. Publ. de Circ., No. 63 Copenhagen.

Lee, R. M. 1920. A Review of the Methods of Age and Growth Determination in Fishes. Fishery Invest., Ser. II. Vol. IV, No. 2. London.

Meek, A. 1916. The Scales of the Herring and their Value as an Aid to Investigation. Dove Mar. Lab. Rep., New Ser. V. Newcastle.

Molander, A. R. 1918. Studies in the Growth of the Herring. Sv. Hydrogr.-Biol. Komm. Skr. Gothenburg.

Runnstrøm, S. 1936. A Study on the Life History and Migrations of the Norwegian Spring-Herring. Rep. Norw. Fish. and Marine Invest., Vol. V, No. 2. Bergen.

Segerstråle, Curt. 1921. Lämna årsringarne i fjällen hos vora vanliga sötvattenfiskar en tilförlitlig bild av fiskens tillväxt under olika ålders-stadier? Acta Soc. Faun. Flor. Fenn., 48, 6.

Thompson, H. 1926. Haddock Biology III. Fisheries Scotland, Sci. Invest., II. Edinburgh.

Watkin, E. Emrys. 1925. Investigations on Cardigan Bay Herring. Rep. Mar. and Fr. Water Invest. Univ. Coll. Wales, Aberystwyth, Vol. I.

Winge, Ø. 1915. On the Value of the Rings in the Scales of the Cod as a Means of Age-Determination. Meddel. Komm. Havunders. Fisk., IV, 8. Copenhagen.

4

ON THE RELATION BETWEEN THE GROWTH OF THE FISH AND THE GROWTH OF THE SCALES.

BY

PER OTTESTAD.

THE method according to which the relative breadth of the growth-zones in the fish scales is used to determine the growth of the fish itself is based on the conception that those structures in the scales which are caused by annual fluctuations in environment furnish a review of the life history of the fish, and particularly of its growth. Hitherto, growth calculations have mainly been based by scientists on the hypothesis that the ratio of fish length to length of scale is independent of the age of the fish, that is to say, that the fish and the scales grow proportionately. When this hypothesis was first advanced, it was quite clearly understood that its validity required careful study. A great number of investigations into the question have been made but, so far, the problem of whether the hypothesis is, or is not, in accord with the facts has not been solved.

The object of the present investigation is not to prove this hypothesis but merely to discuss the various methods which have been adopted to deal with observations in the study of the relation of the growth of the fish to that of the scale. Taking the position as it is, it is, in my opinion, of fundamental importance to ascertain why the various investigations yielded results differing from each other. In view of the multitude of papers dealing with this subject I shall confine my references to a limited selection, since many scientists have employed the same method. Thus the problem before us is, whether or not a certain method is suitable, and if so what are the principles of observation which must be laid down in order to permit indisputable conclusions to be drawn. A critical discussion of this kind may facilitate the planning of new investigations.

The hypothesis that the growths of the fish and the scale are proportional can be expressed in simple mathematical terms as follows:— If l is the length of the fish at any age and s is the corresponding length of a special radius (or other linear dimension) of a particular scale, the hypothesis can be expressed in the equation

$$l = k \cdot s$$

in which k is a constant factor, independent of the age of the individual fish.

If the ratio of fish length to scale length is dependent on the age of the fish, k is a function of the age. Now, s is also a function of the age and, therefore, k can be taken as a function of s, thus giving

$$l = k \cdot s = f(s) \cdot s \text{ or } f(s) = k = \frac{l}{s}$$

First and foremost it should be borne in mind that k has different values for the various scales of the same fish, in as much as the size of the scales varies. The value of k is also different for the various scale radii in the same scale for the reason that in shape the scale is not a circle. If we take a special scale and as a measure of the size of this scale we select a particular radius we know that the ratio of fish length to scale length varies from fish to fish. A description of such a variation within a certain age-group is given in Table 1. The data are taken from Lea (1910).

Table 1.

The Frequency Distribution of the Ratio $k = \frac{l}{s}$ within a Sample of 6-year-old Norwegian Herring.

k	25—26	26—27	27—28	28—29	29—30	30—31	31—32
Frequency	6	16	56	77	40	15	8

It will be seen that the ratio k fluctuates between 25 and 32.

It should also be mentioned here that there is a positive correlation between the size of the fish and the size of the scale (Ottestad 1934). A task of greater importance in this connexion, however, is the investigation of the question whether or not there is some correlation between the length of the fish and the ratio $k = \frac{l}{s}$. Lea (1910) has published a great number of paired observations of l and s of Norwegian herring. This material is not ideal, but as I have found nothing more suitable, I have no option but to use it. The material is arranged in age-groups and Table 2 shows the values of the correlation coefficient between l and k for 4 age-groups.

Table 2.

Correlation Coefficient between *l* and *k*.

Age	r	Number of observations.
year	+ 0·18	74
years	+ 0·23	36
—	+ 0·26	33
—	+ 0·19	218

be seen that the numbers of observations are hat small, particularly in the 2- and 5-year . The value of the correlation coefficient, r, is nearly the same for the various age- , and there is no doubt that there is a e correlation between *l* and *k*, i.e., the large ve, on the whole, relatively smaller scales e smaller fish.

he of the correlation tables can be replaced torily by the Gaussian frequency function. efore, we had only one value of the correla- efficient, it is doubtful if it would be correct that there is a positive correlation between *k*. In this case, however, we have, so to 4 repeated observations of *r* and these d observations are nearly the same. There me groupings of data which seem to show ends to increase slightly with increasing age, ether this is so it is impossible to say with ty.

re are also other observations which indicate ere is a positive correlation between *l* and *k*. here confine myself to mentioning that L e e has found that "there is a tendency for the st fish at any size to have smaller scales than ish ....".

will be shown subsequently that this positive tion between the fish length and the scale has a fundamental bearing on the problem liscussion. In connexion with new investiga- f the ratio of fish length to scale length it great importance to study this correlation n further. It should be borne in mind, r, that undoubtedly there is also a hical variation in the relative scale size. As equence of the positive correlation between , *k* should, within smaller populations, have raphical variation which, to some extent, run parallel to the variation in *l*. But there reason to believe that over wider geogra- areas there are greater variations in the of *k*. The number of scales has some hical variation, e.g., the number of keeled And there is reason for believing that the n in the number of scales exerts some ce on the variation in *k*. T h o m p s o n has shown that there is probably some nce in the relative scale size between the ic and the North Sea haddock. The Icelandic are slightly larger relatively to the fish than those of the North Sea fish.

A survey of the numerous papers which have a bearing on the problem under discussion speedily convinces us that there are only a few guiding principles for the investigations. It is sufficient, therefore, to take a few of these investigations and deal with the methods adopted.

The fundamental problem is to ascertain whether the ratio of fish length to scale length is or is not dependent on the age of the fish. If for a single fish paired observations of the fish length (l) and the scale length (s) of a certain selected scale in different ages could be procured, it would be possible to find whether the ratio $k = l : s$ alters with the age of the fish. To procure such paired observations, however, is not an easy task. It may be possible in the case of species which can be kept in tanks where the environment undergoes great periodical fluctuations. It is known that the growth-rate is positively correlated with the temperature of the environment. By measuring the length of the fish at times when the temperature is low, and, at the end of the experiment, measuring the length of the radius from the centre to the various "winter" rings in a particular scale, we can obtain paired observations of l and s. An experiment of this nature, however, must of necessity occupy several years. I am not aware that any such experiments have been made, but I consider that such an attempt would be worth while. In any event there does not appear to be any better method of solving the problem. On each occasion on which the fish is measured for length, it is desirable that scales should be taken from it. If this is done, it becomes possible to ascertain whether the growth of the scales is checked on these occasions.

An experiment of another kind may be made with species which can be marked and liberated. W i n g e (1915) investigated 4 cod fish which during the period between capture and recapture had grown from 40 to 55 cm., from 31 to 43 cm., from 40 to 51 cm., and from 43 to 66 cm. As he could identify in the scales of the recaptured fish the position of the edge of the scales at first capture, he was able to measure the growth increments of the scales between capture and recapture. In this way is was proved that the fish and the scales had grown proportionally. This information, however, is not satisfactory. Even if the scales and the fish grow proportionally during such a short period of life, it is not certain that there is also proportional growth at any moment of the total span of life.

It may nevertheless be possible to use this method in a more satisfactory manner. We may select a number of fish of the same species, the size of which at the time of first capture covers nearly the whole range of size variation of the species. In that case we should be able to study the relation between the growth of the fish and the growth of the scales at any age of the fish.

Another way of applying the experimental

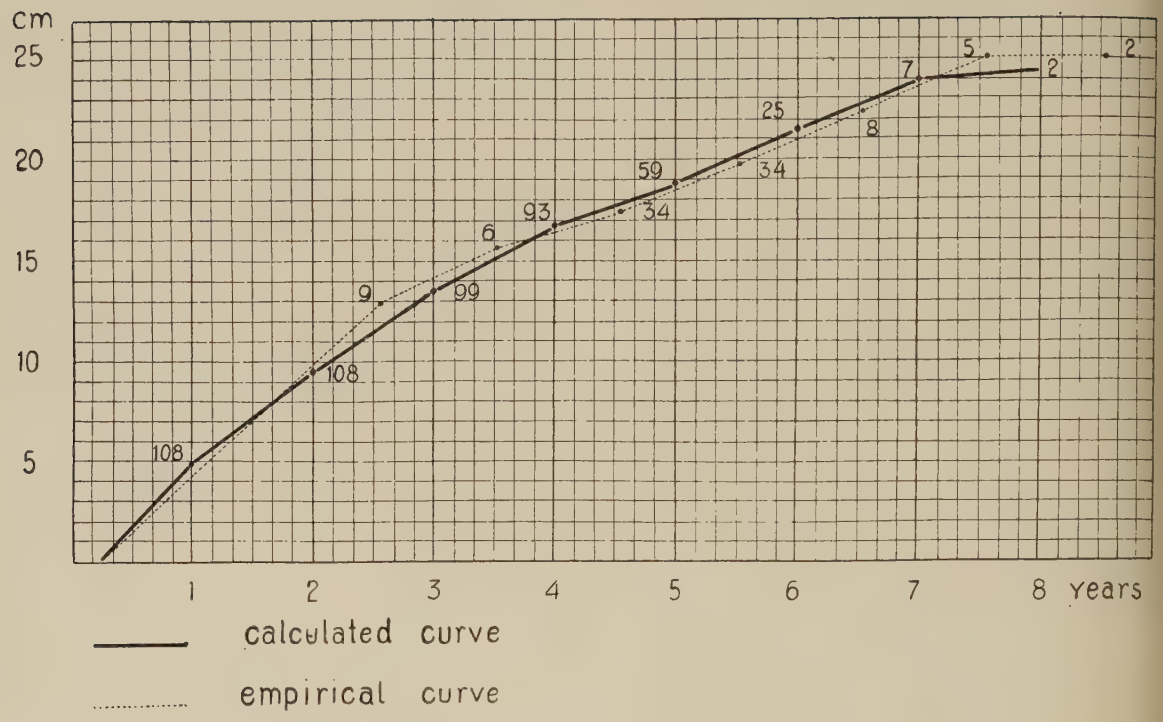


Fig. 1. Empirical and calculated growth curves of trout.
From D a h l (1911).

method would be to calculate the fish length at the age of 1, 2, 3, 4, ... years both at the time of capture and on recapture. If the correct calculation formula is used, the calculated lengths should be the same in both cases.

In both cases, however, it is of fundamental importance that the time interval between first capture and recapture should be as long as possible. The longer the interval, the greater the force of the observations as proof or disproof of a given hypothesis as to the relationship between the growth of the fish and the growth of the scales.

The advantage of the experimental method is that we investigate the relationship between the fish-growth and the scale-growth of a single fish. Most scientists, however, have adopted methods of another kind. The paired observations of the values of l and s of an individual fish are replaced by mass observations. In these cases we are always confronted with the serious difficulty that we are in no case sure, or able, to make sure, that the various age-groups or length-groups represent different stages in the life history of one and the same population.

The first paper which I select is one by D a h l (1911) which deals with age and growth of salmon and trout in Norway. The salmon is a very interesting species in this connexion, in view of the large alteration of the growth-rate at the time when the fish migrate from the rivers to the sea. This alteration in environment can be identified in the scales as a migration ring. D a h l measured the length of the scales from the centre to the migration ring and the length from the centre to the edge of the scale in a sample of sea salmon. By means of these measurements he was able to calculate the length of the fish at the age when it migrated from the river to the sea. He then used the formula of proportional growth of the fish and the scales. In this way he found that the average calculated length of the fish in the migratory stage was very nearly the same as the average length of salmon actually measured in the migration stage.

D a h l (1911) has also compared calculated lengths and directly measured lengths of trout. Fig. 1 shows the calculated growth-curve and the growth-curve constructed on direct measurements. It will be seen that the two curves are nearly identical. This agreement strongly supports the hypothesis of proportional growth of fish and scales, yet it is not conclusive because there is no evidence for assuming that these two growth-curves represent the average growth of individuals from one and the same population. It should further be remembered, as D a h l himself remarks, that

es in Fig. 1 are not real growth-curves. The owth-curve is of a periodic nature owing to ual cycle in the growth.

e (1912) finds that the average calculated are subject to a constant discrepancy which ls "the phenomenon of apparent change in rate". L e a (1913) is of the opinion that enomenon is due to selective sampling. myself (O t t e s t a d 1934) proved that the enon discussed by L e e for the Norwegian material is explicable if only a certain type of a single year-class (1904) is con-

Table 3 shows the average yearly incre- n length (t_1, t_2, t_3 ....) of the A-type[1]) year-class 1904 as spawning herring on the ast of Norway in various years from 1909 916.

vill be seen from this table that there is riation in the calculated growth-rate, though riation does not appear to have any parti- rend. If the calculation formula, which in e has been based on the hypothesis of con- tio of fish length to scale length, did not with the facts, a marked trend of the n would be expected.

hould also be borne in mind that there is on to believe that the material relating to t years represents exactly the same ion. The A-type, which consists of the uals with decreasing yearly increments in is only a first approximation to a population eneous with regard to growth. The main s that the A-type is a more homogeneous han the total population, and it is quite hat the phenomenon described by L e e is lly eliminated in this smaller population. earches into the correlation between the fish and the size of the scale have played a very great part in the discussion of the relationship between the growth of the fish and that of the scales. Briefly, the method is to collect a large number of paired observations of l and s of fish with the greatest possible length or age variation. The paired observations of l and s are arranged in a correlation table, and in most cases the averages of l are calculated for every scale size or class of scale size. In this way average lengths are obtained which can be represented by a curve in a cartesian co-ordinate system, with the fish length as abscissa and the scale size as ordinate. This curve then describes the manner in which the average fish length increases with the increase of the scale size. In some cases the averages of l are not calculated. Each fish is represented in a cartesian co-ordinate system by a point. In this way we obtain a point cluster which can be represented by a curve drawn through the mean-points of l corresponding to each scale size.

As an example of this kind of investigation I will reproduce a diagram from C r e a s e r (1926). In this diagram (Fig. 2) the fish length is entered on the abscissa axis and the scale radius on the ordinate axis. Through the point cluster a curve is drawn which represents the functional relationship between the average fish length and the size of the scale.

Now, it is clearly stated that in the opinion of the author and of other scientists who have used the same method, this curve should be a straight line through the origin ($l = 0$, $s = 0$) if the ratio of fish length to scale size is constant for each single fish. As this curve (Fig. 2) is not a straight line and apparently does not pass through the origin, C r e a s e r concludes that the ratio of fish length is not constant but is a function of the age of the fish. I will return to this question below. It should be understood, however, that it is no easy task to find the point where a curve such as this intersects the l-axis. Apparently if we extra-

[1]) The growth-type A is defined as the fish which have decreasing yearly increments in length with increase of age.

Table 3.

The Mean Values of t_1, t_2, t_3, etc. for the A-Type of the Year-Class 1904 as Spring Herring, taken on the west coast of Norway. N stands for the number of individuals examined. From O t t e s t a d (1934).

Year	Sample No.	N	t_1	t_2	t_3	t_4	t_5	t_6	t_7	t_8	t_9	t_{10}	t_{11}	t_{12}
1909	22	89	9·4	7·9	6·0	3·5	2·4							
—	23	43	9·1	7·9	6·2	3·5	2·4							
1911	24	110	9·5	7·9	6·0	3·6	2·3	1·3	0·9					
1912	25	59	8·9	7·4	6·0	4·2	1·8	1·4	1·0	0·9				
—	26	49	9·2	7·6	5·9	3·6	2·2	1·3	0·9	0·9				
—	27	65	8·7	7·2	5·9	3·7	2·5	1·4	0·9	0·7				
1914	28	42	9·2	7·7	6·1	3·5	2·1	1·2	1·0	0·7	0·8	0·5		
—	29	41	8·7	7·4	6·2	3·5	2·3	1·3	1·0	0·7	0·8	0·4		
—	30	80	8·8	7·4	5·9	3·6	2·2	1·4	1·0	0·8	0·8	0·5		
1915	31	78	8·8	7·4	5·9	3·6	2·3	1·3	0·9	0·8	0·8	0·5	0·6	
—	32	77	9·0	7·4	5·8	3·6	2·2	1·3	1·0	0·7	0·8	0·5	0·5	
1916	33	142	9·5	7·2	5·7	3·3	2·0	1·1	0·9	0·7	0·7	0·6	0·5	0·4

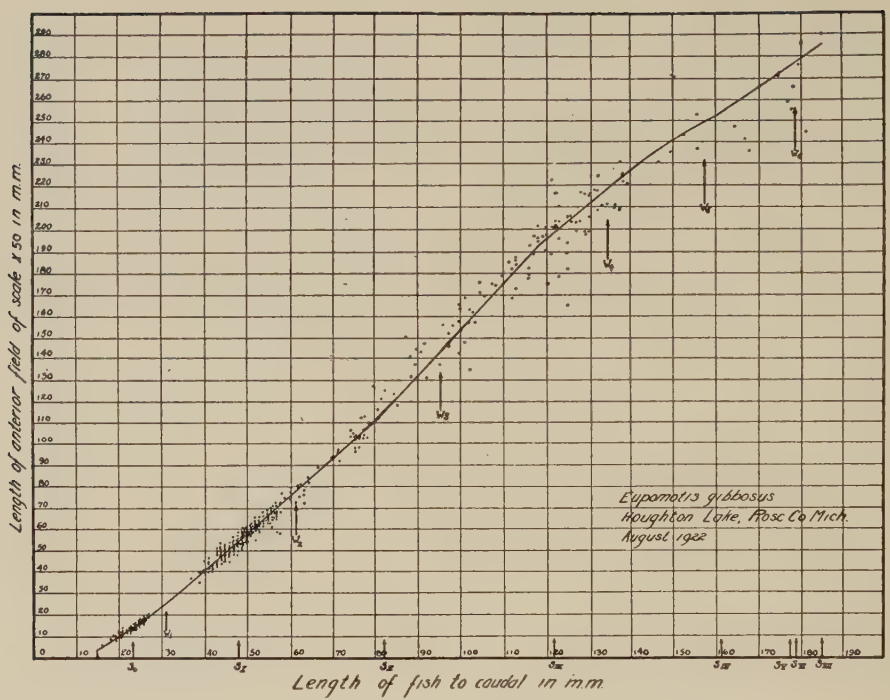


Fig. 2. The length of the anterior field of the special scale in mm. × 50 (ordinates) as compared with the length of the fish to the base of the caudal fin mm. (abscissae). The dots indicate the position of each reading for all the specimens from Houghton Lake. From Creaser (1926).

polate on this curve it will intersect the l-axis at the point of $l =$ ca. 10 mm. But it should be remembered that when we extrapolate on this curve to the intersection of the l-axis at the point $l = 10$ mm., we are acting on the supposition that the curve is straight. But the curve is not a straight line and this makes the question of its intersection on the l-axis much more difficult to answer. It should also be remembered that in this diagram (Fig. 2) the s-values are multiplied by the factor 50. If the absolute unit were used as the unit of the ordinate axis, the curve would pass close to the l-axis, and it would be very difficult to determine the point at which the curve intersects the l-axis.

Let us return, however, to the fundamental problem and ask ourselves the following question:— Are there sound reasons for assuming that the curve describing the functional relationship between the scale size and the average fish length is a straight line through the origin, if the ratio of fish length to scale size is constant for each single fish? The easiest method of supplying an answer to this question is undoubtedly to construct this line theoretically and find the conditions under which it is a straight line through the origin.

Lea (1933) has most clearly shown that the regression line between l and s has no direct bearing on the problem under discussion. I myself have demonstrated the same thing in an earlier paper (Ottestad 1934). The curve in Fig. 2, however, is not a regression line in ordinary terms. Corresponding to Creaser's data there are more regression lines which would be found if the data were arranged in smaller groups, for example age-groups. Granting certain assumptions, however, we are able to reconstruct the line theoretically.

Let us assume that we are able to observe N fish from birth to the maximum age, and let us also assume that we can measure the length of a certain radius (s) in a specially selected scale at every age of the fish. The observations of l and s which we obtain at a precise moment can now be plotted in a cartesian co-ordinate system where l is on the abscissa axis and s on the ordinate axis. In this system each fish is then represented by a point and the N points together form a point cluster.

If the ratio of fish length to scale length is a constant for each single fish, i.e., $l = k \cdot s$, we obtain

$$\overline{l} \quad \overline{k} \cdot \overline{s} + r \cdot \sigma_k \cdot \sigma_s \qquad (1$$

where $\overline{l}$ is the mean value of l, $\overline{k}$ the mean value of k, $\overline{s}$ the mean value of s, r the correlation coefficient between s and k, σ_k and σ_s the standard deviations of k and s.

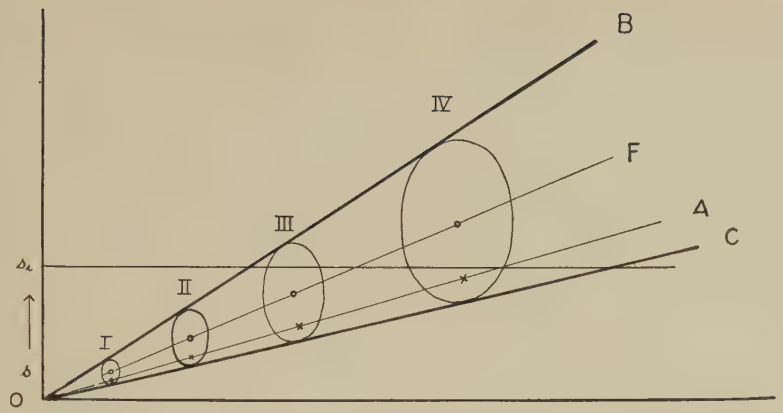


Fig. 3. For explanation see text.

hese N paired observations of l and s are l at various ages, we obtain more of these usters, each of which refers to a certain age. 3 four such point clusters (I, II, III, IV) wn. According to the assumption that the fish length to scale length is constant for gle fish, every point cluster is bound to lie he angle BOC, and each cluster must have one point common to both straight lines OC. In each cluster a particular fish is ted by a point, and these points lie on the raight line through zero. OA is such an al line.

ach point cluster there is a mid-point the ates of which are the mean value of l ($\bar{l}$) mean value of s ($\bar{s}$). Through these mid- e can draw a line the equation of which is formula (I). According to the assumption, σ_k are constants in this equation, l, s, r are variables.

we are not able to represent r and σ_s as s of s, this equation represents an unknown may be possible to find the exact functional ship between $\bar{l}$ and $\bar{s}$ with the aid of certain assumptions. But to treat the problem along es is of no interest as it is hardly possible practical effect to such an experiment as scribed above. We can, however, arrange obtained by means of this hypothetical ent in groups according to new principles. arrange them in groups which are rized by a constant value of s, that is to fish with $s = s_i$ form a new group. One of groups will contain individuals from more older groups which are characterized by e of the fish. The group for $s = s_i$ (Fig. 3) tain individuals from both group III and V.

hese new groups we shall have $\bar{s} = s$, $= 0$, and the equation of the mid-point

$$\bar{l} = \bar{k} \cdot s \qquad \text{(II)}$$

In equation (I) $\bar{k}$ is a constant according to our assumptions. In equation (II) $\bar{k}$ is also a constant if the observations of the paired values of l and s are made continuously, i.e., every s-group contains all N individuals.

If the observations of l and s are made intermittently, in other words, if there is a pause between two neighbouring observations, $\bar{k}$ will be a variable quantity, and we can express it as a function of s.

In the first case — continuous observations — the mid-point line is a straight line through the origin. In the second case the mid-point line will be a periodic function of s, with varying periods. The trend of this periodic function, however, may be a straight line through the origin.

This deduction is based on the assumption that the younger and the elder groups are always represented by the same individuals (number N). Turning now to the position as it actually is we must remember that the various age-groups in the material are not represented by the same individuals. The observations of l and s are not repeated in various ages of the same individuals. The observations are l and s of different age-classes. Such a material will very often — and as a rule — be composed of age-classes showing some trend in one direction or another. The rule is certainly that the younger age-classes are represented by the largest individuals of the particular age-class, i.e., those individuals which have the greatest growth-rates.

The elder age-groups may, or may not, be more representative of the population in the sea. The trend in the sampling may be due to the use of selective gear, but it may also be due to the fact that the various growth-types of fish have different geographical distributions.

As we know that the ratio of fish length to

scale length is positively correlated with the length of the fish, it is obvious that sampling with a systematic tendency to error in respect of the length of the fish is also a sampling with a systematic tendency to error in respect to the ratio $k = \frac{l}{s}$.

Let us assume that we are fishing with selective gear. The youngest age-groups are represented by the fastest growing individuals, but the effect of the selective sampling decreases with the increase in age or size. In such a case the line which represents the functional relationship between the scale size (s) and the corresponding average length of the fish (l) must be a line of the same nature as the hyperbolic line. This line will intersect the l-axis at some positive distance from the origin. But such a relation between the scale size and the corresponding average fish length may just as well be due to other circumstances. It is, however, of very little or no interest to enter into these difficult matters in greater detail.

The direct conclusion to be drawn from this discussion, however, is the very simple one that the study of the nature of the relationship between the size of the scale and the corresponding average fish length cannot furnish us with proof or disproof of the hypothesis of the constant ratio of fish length to scale length of the individual fish, nor can we in this way discover the relationship between the growth of the fish and that of its scales.

Lea (1910) compared average values of the ratio of fish length to scale length of various age-classes of Norwegian herring. The observations (l and s) were collected in the manner described above, but Lea treated these observations in a different way. The material was arranged in age-groups. For each single individual the ratio (k) was calculated and the average ratio was calculated for each age-group. These averages are reproduced in Table 4.

Table 4.

The Average Ratio of Fish Length to Scale Length. From Lea (1910).

Age	$\bar{k}$	Number of observations.
1 year	29·7	74
2 years	29·0	36
3 —	27·1	2
4 —	27·4	11
5 —	28·7	33
6 —	28·3	218
7 —	28·5	19
8 —	28·4	2
9 —	27·9	3
10 —	28·6	6
11 —	27·8	7
12 —	28·3	1

It will be seen that the number of observations is somewhat small. But in the case of the 1-year, 2-year, 5-year, and 6-year groups the observations are so numerous that the averages can be relied upon.

The table shows that, on the whole, the average decrease with increase in age. From this fact Lea concludes that the scale grows relatively quicker than the fish length. This conclusion is obviously open to the following objections. The table shows that the 1-year-old herring have, on the average, relatively smaller scales than, for example, the 6-year-old herring. Now we know that these 1-year-old herring are fished on the west coast of Norway and we are also well aware that they are not immigrant fish, as the large migrations begin at a higher age. These one-year-old herring, therefore, are west coast herring. The older age-classes (e.g. the 6-year group), on the other hand, are a mixture of fish which have spent their first years of life in the various parts of the coastal waters from the most southerly regions up to Finmark. We may therefore also take the tendency to decrease in the average ratio $k = \frac{l}{s}$ as a proof that the herring from the west coast have relatively smaller scales on the average than the herring from more northerly parts of the coast. This explanation is strongly supported by the finding that the ratio k is positively correlated with the fish length. This finding is derived from investigations of smaller populations than the total population of the Norwegian herring. It is, therefore, a task for further research to investigate the problem whether the correlation between l and k can be extended to larger populations or, in other words, whether the correlation also means a geographical variation in k. But taking into consideration all the information we have concerning the Norwegian herring population, we may say (cf. Table 2) that there is a very strong indication of a geographical variation in k, that is to say, that the slow-growing herring from the northern localities have relatively larger scales than the faster growing herring from more southerly localities. In Table 4 the 1-year group is composed of west coast herring, but the 6-year group is composed of both west coast herring and herring from more northerly localities.

If, therefore, we assume that the ratio of fish length to scale length is constant for the individual herring, it is obvious that the average ratio must tend to decrease with increase in age as long as the data used are collected in a manner similar to that of the data in Table 4.

The conclusion to be drawn from this discussion is not that Table 4 can be taken as a proof of the hypothesis that the growth of the herring is proportional to the growth of the scales, but that the tendency of the average ratio to decrease with increase in age is in very good agreement with that hypothesis.

In this short paper I have endeavoured to assess the value of the various methods which have been

red in the study of the functional relationship n the growth of the fish and the growth of ales, and also to estimate the value of the yielded by the various investigations based hese methods.

e conclusion to be drawn from this study is has not yet been finally determined what nship exists between the growth of the fish at of its scales. In my opinion, however, are so many indirect proofs or indications e fish and the scales grow proportionally, e may accept this as a fact. When it is said e scales grow proportionally with the fish, es not mean that this relationship is a straight mathematical terms. It means that the ratio length to scale length is approximately con- iroughout the whole life history of the fish.

Literature cited.

er, Charles W. 1926. The Structure and wth of the Scales of Fishes in Relation to the Inter- tion of their Life-History, with special Reference e Sunfish Eupomotis gibbosus. Museum of Zoology, ersity of Michigan, Miscellaneous Publ. No. 17,

Knut. 1911. The Age and Growth of Salmon and t in Norway as shown by their Scales. Salmon and t Assoc. London, 1911.

Lea, Einar. 1910. Contributions to the Methodics in Herring-Investigations. Cons. Perm. Internat. p. L'Explor. de la Mer, Publ. de Circ., No. 53, Copenhague, 1910.

Lea, Einar. 1913. Further Studies concerning the Methods of calculating the Growth of Herrings. Cons. Perm. Internat. p. l'Explor. de la Mer. Publ. de Circ. No. 66, Copenhague, 1913.

Lea, Einar. 1933. Connected Frequency-Distributions. A preliminar Account. Fiskeridirektoratets Skr. (Rep. Norw. Fish. and Mar. Invest., Vol. IV, No. 2), Bergen, 1933.

Lee, Rosa M. 1912. An Investigation into the Methods of Growth Determination in Fishes. Cons. Internat. p. l'Explor. de la Mer. Publ. Circ. No. 63. 1912.

Lee, Rosa M. 1920. A Review of the Methods of Age and Growth Determination in Fishes by Means of Scales. Ministry of Agric. and Fish., Fish. Invest. Vol. 4, No. 2. 1920.

Ottestad, Per. 1934. Statistical Analysis of the Norwegian Herring Population. Rapp. et Proc. Verb. LXXXVIII, Copenhague, 1934.

Thompson, Harold. 1929. General Features in the Biology of the Haddock (*Gadus æglefinus* L.) in Icelandic Waters in the Period 1903—1926. Fish. Board for Scotland Scient. Invest. No. V. Edinburgh, 1929.

Winge, Ø. 1915. On the Value of the Rings in the Scales of the Cod as a Means of Age Determination. Medd. fra Komm. Havundersøgelser. Ser. Fiskeri, B. IV. Copenhague, 1915.

5

ON DIVERSITY OF GROWTH IN FISH.

BY

OSCAR SUND.

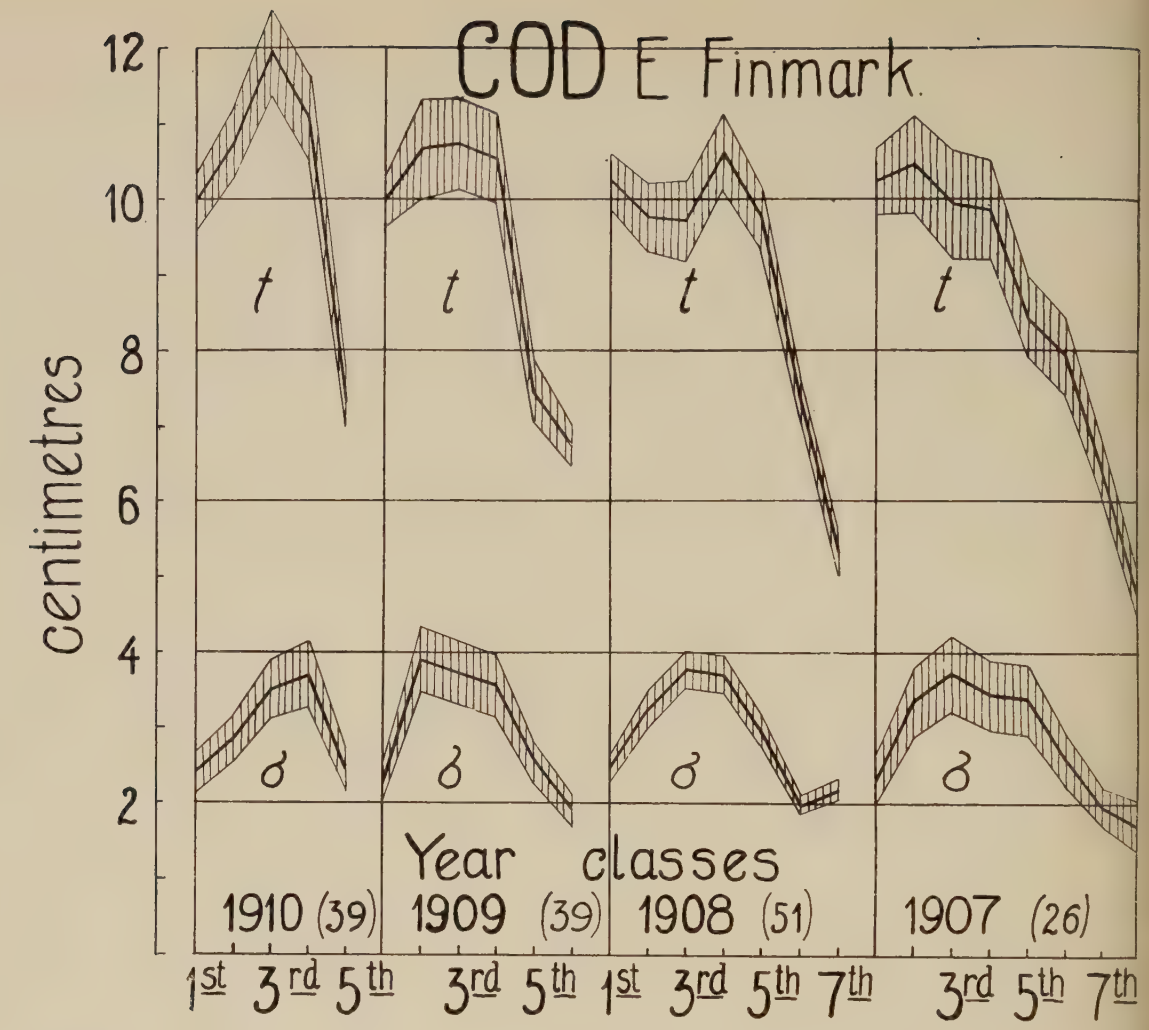

COD E Finmark.
centimetres
12
10
8
6
4
2
t
t
t
t
♂
♂
♂
♂
Year classes
1910 (39)
1909 (39)
1908 (51)
1907 (26)
1st 3rd 5th
3rd 5th
1st 3rd 5th 7th
3rd 5th 7th
t
♂

Fig 1

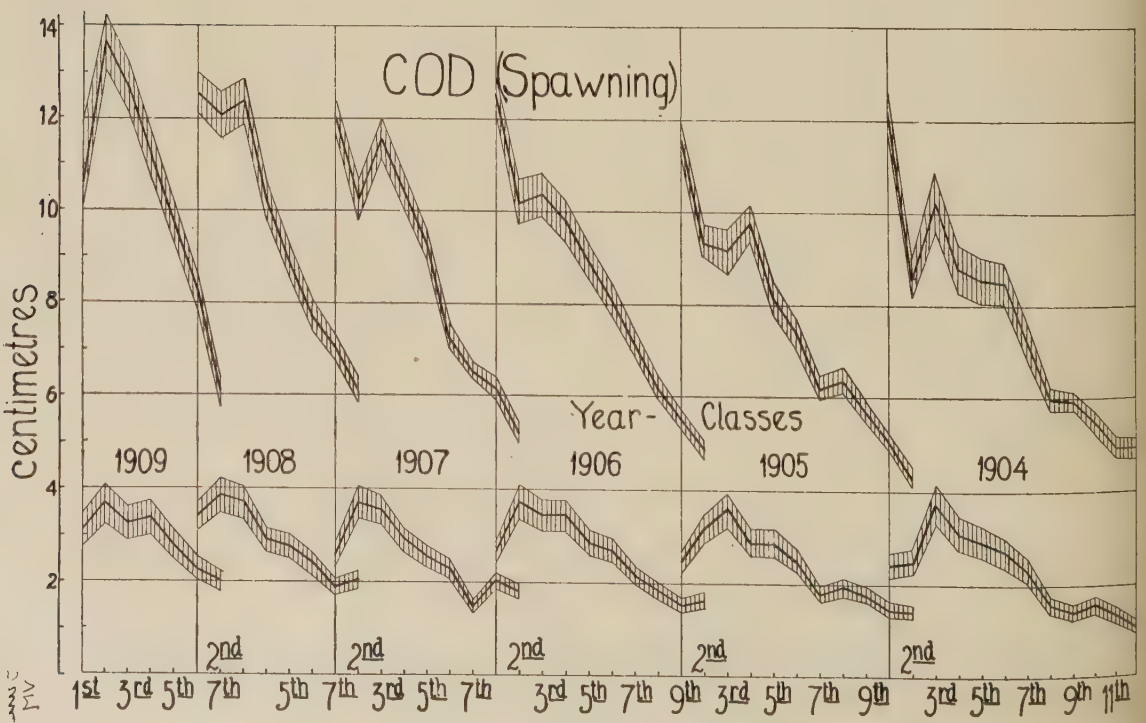
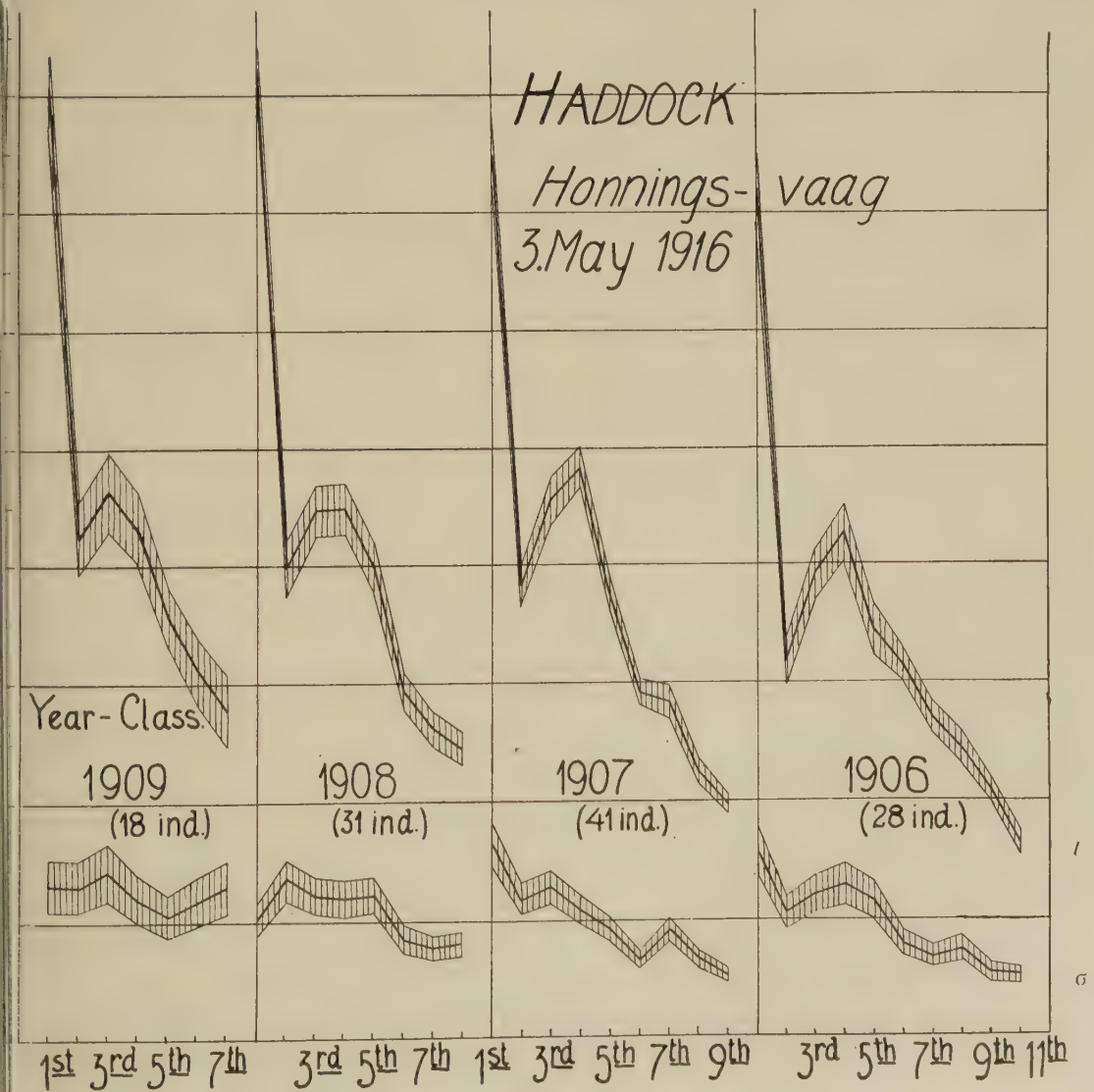

COD (Spawning)
centimetres
14
12
10
8
6
4
2
Year-Classes
1909
1908
1907
1906
1905
1904
2nd
2nd
2nd
2nd
2nd
1st 3rd 5th 7th
5th 7th
3rd 5th 7th
3rd 5th 7th 9th
3rd 5th 7th 9th
3rd 5th 7th 9th 11th
t
♂

Fig. 2

N the assumption that the yearly increments in length can be ascertained by measuring the width of the scale-zones it is apparent t only do these increments fluctuate in a indicating important changes in the well- f the fish, and particularly in their means istence, but that their standard deviation, or ", seems to offer a useful clue to one aspect history of the particular community repre- by the sample.

A wide spread of increment values, therefore, would appear to indicate that the fish only congregated for shoaling shortly before they were caught, in as much as common conditions of life have not had time to exert any influence tending to make for uniformity of growth. On the other hand, uniformity of growth, or a more moderate "spread" of the increments, may generally be accepted as an indication of a comparatively long period of community of habitat.



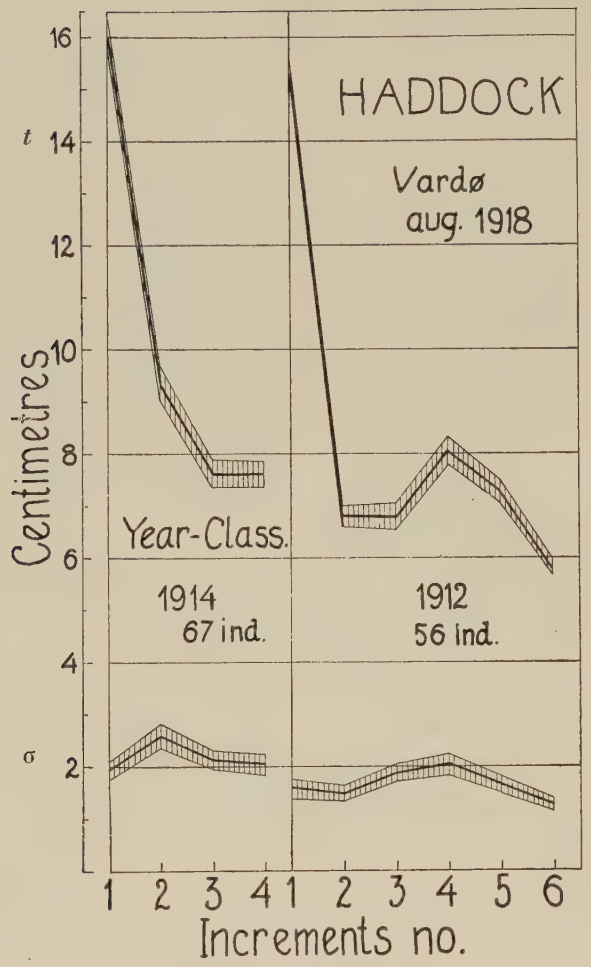


Fig. 4.

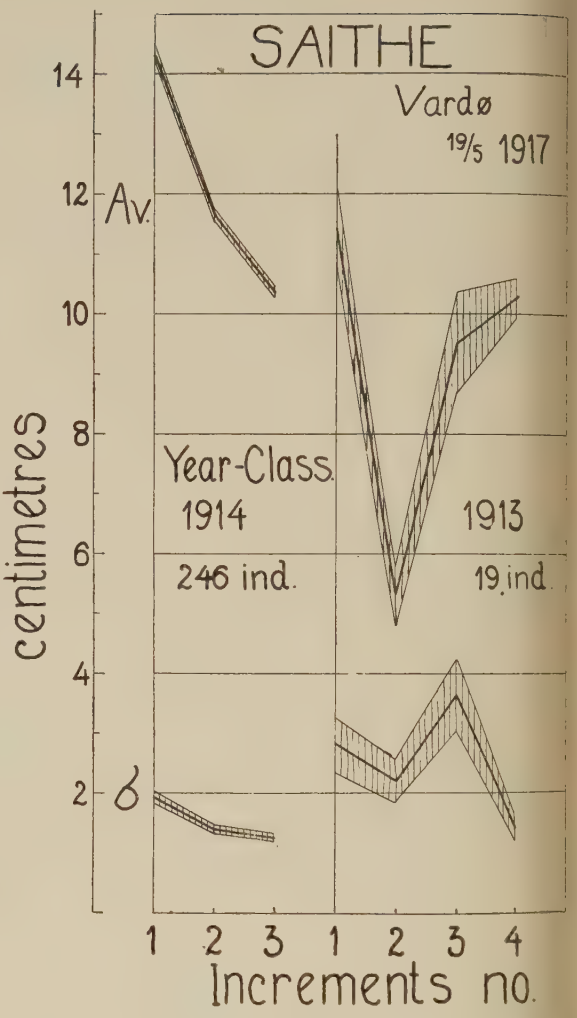


Fig. 5.

On the basis of this assumption we present in the form of graphs the calculated length increments and their standard deviation in samples of cod, haddock, and saithe.

In our opinion this method of presentation, in which also the standard errors of the two values are shown, enables a better idea to be obtained of the growth and its variability than from merely numerical tables.

From the "spread" it would appear that the three species differ from each other in the following manner:—

The **cod** show, on the whole, a gradually increasing resemblance to each other of the individuals comprising each year-class in the sample, indicative, in all probability, of a similarity of conditions in the areas in which the populations, from which the sample has been collected, have been formed by gradual accumulation or congregation.

In the case of the **haddock**, a fish which has a long pelagic life, the stock appears to be composed of individuals spawned in a great diversity of areas and carried by the currents in widely differing directions from the North Sea to the Barents Sea. This would explain the great variety in the size of the fish after the first year. As a general rule the spread calculated for the subsequent years of the life of a year-class (individuals born in the same calender year) becomes smaller with the increasing age of the fish. This indicates that once a shoal is formed its members tend to remain in company with each other or to keep to the same habitat.

Among **saithe** we find a low variability in growth right from the beginning. This is in keeping with the well-known propensity of these fish to shoal strictly among themselves and thus live under the most uniform conditions possible as regards means of subsistence and general well-being.

6

IANGES IN MEAN AGE AND GROWTH-RATE OF THE YEAR-CLASSES IN THE ARCTO-NORWEGIAN STOCK OF COD.

BY

GUNNAR ROLLEFSEN

E Arcto-Norwegian stock of cod denotes the tock of cod which, in its immature stage, loddetorsk", is to be found in the Barents which in its sexually mature stage makes e spawning migrations and then occurs off wegian coast from the North Cape to Stadt ne name of "Skrei". This stock of cod has the subject of exhaustive investigations by ians (S a r s, H j o r t, S u n d), and many which have subsequently become of general ance have been discovered in connexion with ly of this important population of fish.

nerly the age analyses of "skrei" and orsk" were based on scale readings. In owever, the author studied the comparative ity of the otoliths and the scales as means rmining age, and the result of this favoured liths. For young fish there was complete between the number of zones on the otoliths scales, and no difficulties were experienced blishing correspondence between the first nost) zones in scales and otoliths, even in e of older fish. The outer zones of the however, became more and more difficult the closer the periphery of the scale was ched, whereas the outer zones of the otoliths a rule even easier to distinguish than the ones.

collection of age data from this investig- was re-arranged in such a manner that the mphasis was laid on otolith material, and pting various methods the reading of the was rendered both speedier and cheaper e reading of the scales had been.

ring the past six years a comparatively large on of otoliths of the spawning "skrei" as und in Lofoten has been procured, and in n to age data, observations of the length of li idual fish, its weight in a round and a condition, and its sex and spawning stages, een made.

employment of the otoliths of the "skrei" e determinations has proved a profitable in many ways. It has demonstrated that oliths indicate a valuable morphological er which can serve to distinguish the local f coastal cod from the temporarily occurring "skrei", and the otoliths have also contributed usefully to the understanding of the recruitment and mortality of the "skrei" stock. These problems, however, will be dealt with separately in two works which are now in course of preparation. We will, on this occasion, merely give a short account of some new findings concerning changes in the internal state of a fish stock, which have a very important bearing on a number of the problems involved in the study of the fluctuations.

When the "skrei" makes its appearance during the early months of the year on the Norwegian coast the majority finds its way into the West Fjord, and it is this inward movement which gives rise to the Lofoten fishery. We have been fortunate in these investigations, in that in Lofoten we were able to study the "skrei" — that is to say, the mature part of the Arcto-Norwegian stock of cod — practically speaking in a pure state, in as much as the cod which belong to the local stock occur in small quantities in proportion to the "skrei". The material forming the basis of these investigations is derived solely from line-caught fish, and as far as possible the material has been collected from the whole of the Lofot area and throughout the entire season. On examination of the data, it soon became apparent that the two sexes should be separated and treated as two different stocks. In the first place a considerable difference in size between male and female fish of the same age could be shown to exist, as has also proved to be the case with other species. Similarly, there was also a difference between the numbers of males and females, as the male fish were most abundant among the young age-classes and the female among the older. Even if this is the first time that this has been established in the case of the "skrei", the phenomenon is so well-known that no further reference will be made to the matter on this occasion.

Our material has brought us into contact with the year-classes which have composed the stock of "skrei" for the past six years. In 1932 we found the last remains of the 1915 year-class, and then in 1937 the first traces of the 1930 year-class. The 1924 year-class we have been able to follow from its eighth to its thirteenth year. Fig. 1 illustrates the percentage distribution of each year-class from 1918

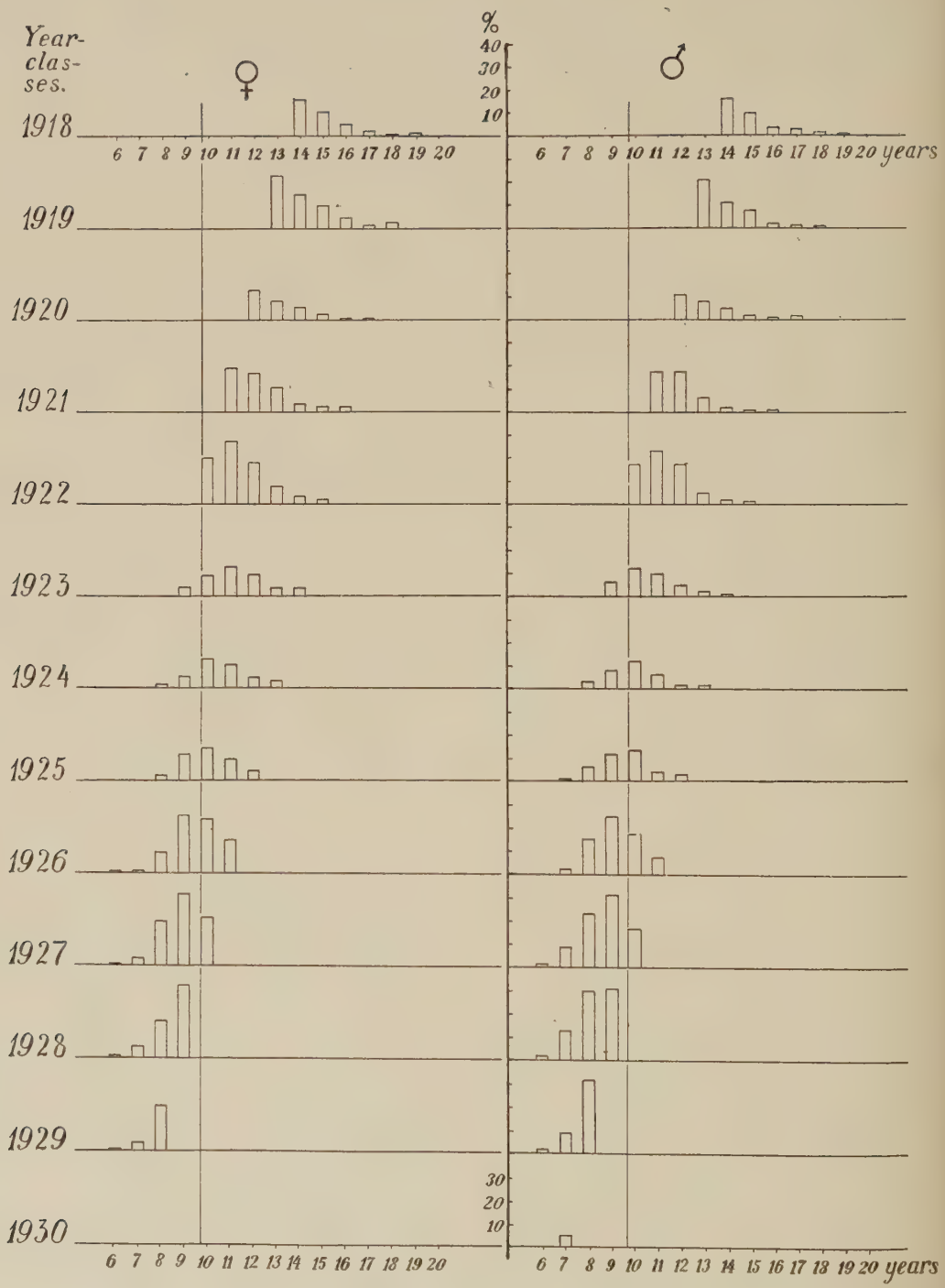

Year-
clas-
ses.
♀
♂
%
40
30
20
10
1918
1919
1920
1921
1922
1923
1924
1925
1926
1927
1928
1929
1930
6 7 8 9 10 11 12 13 14 15 16 17 18 19 20 years

Fig. 1.

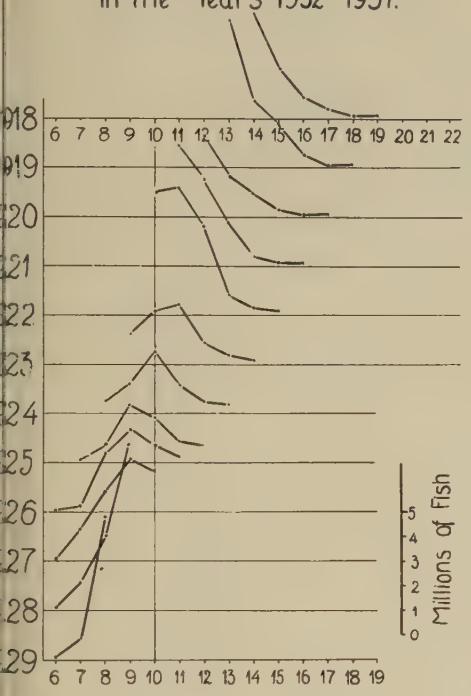


Fig. 2.

0 according to our data, and the two sexes are ented separately. In 1932 the 1919 year-class irteen years old and we observe that the s of this year-class formed 23 % of the al. In 1933 it had declined in importance mounted to about 15 %, and we can follow ar as 1937 when it amounted to about 0·5 %. we look at the year-classes from 1922 to we see that their maximum occurrence in the s declines at an earlier and earlier age in t striking manner. Whereas, in the case of nale fish, the 1922 year-class probably, and 23 year-class undoubtedly, played the greatest t the age of eleven years, the 1926 and 1927 asses seem to play the chief rôle as nine- d fish. Likewise we can observe in the male displacement from a maximum at ten and vears in the case of the 1922 and 1923 a-ses to a maximum at eight and nine years urds the 1927 and 1928 year-classes. It might ly be thought that this displacement arose he mutual effects of richer and poorer year- when their quantitative proportions are sed as percentages, but since the data on Fig. 2 is based cover the entire landings this ation cannot be offered.

Fig. 2 the catch, reckoned in millions of is distributed over the year-classes present according to their percentage strength in the different years. According to this the 1919 year-class yielded about 6 million, as thirteen-year-old fish, and in its fourteenth year about 2·7 million, and so on. The 1922 year-class yielded about 5 million as ten-year-old fish, as eleven-year-olds about the same, as twelve-year-olds it yielded 3·5, as thirteen-year-olds 1, and as fifteen-year-olds about ¼ million fish.

We again observe that, as in Fig. 1, a displacement is exhibited of the age at which the year-classes occur in the greatest quantity in the landings. The 1923 year-class was in greatest abundance present in the tenth and eleventh year, the 1924 in the tenth, the 1925 in the ninth and tenth, and the 1926 in the ninth year. This displacement of the mean age of the "skrei" is clearly discernible, and must therefore be regarded as real. Hence it follows that the year-classes of the "skrei" have been influenced by factors which have caused an absolute reduction of the mean age. This reduction of the mean age can be attributed to three causes, as follows: —

1. Increase of mortality among the sexually mature stock.
2. Accelerated sexual maturation in the immature stock.
3. Increase of mortality among the immature stock.

In order to make the problem more general, we will assume that a stock has a young-fish period of two years and a maturation period of three years (see Fig. 3). During the course of the maturation period all fish become sexually mature, in such a manner that 20 % attain sexual maturity at the end of the third year, 60 % after the termination of the fourth year, and the remaining 20 % at the end of the fifth. We will also presuppose that there is no mortality, and that this is the normal course of sexual maturation.

On the assumption that in the course of a number of years this population has built up a sexually mature stock among which there is an annual mortality of 50 %, the age distribution in this sexually mature stock would be as shown in Fig. 3b, with a mean age of 5·99 years. An increase in the mortality of the sexually mature stock will bring about a change in the mean age, and, as shown in Fig. 3c, a rise in the mortality to 65 % will reduce the mean age to 5·52 years.

If, starting with the same immature stock as before, we assume another rate for sexual maturation. whereby more of the individuals attain sexual maturity at an earlier age, as indicated in Fig. 3d, the sexually mature stock which becomes established in this way will acquire an age distribution such as is shown in Figs. 3e, and f for mortalities of 50 % and 65 % respectively. Under these circumstances the mean age would be depressed to

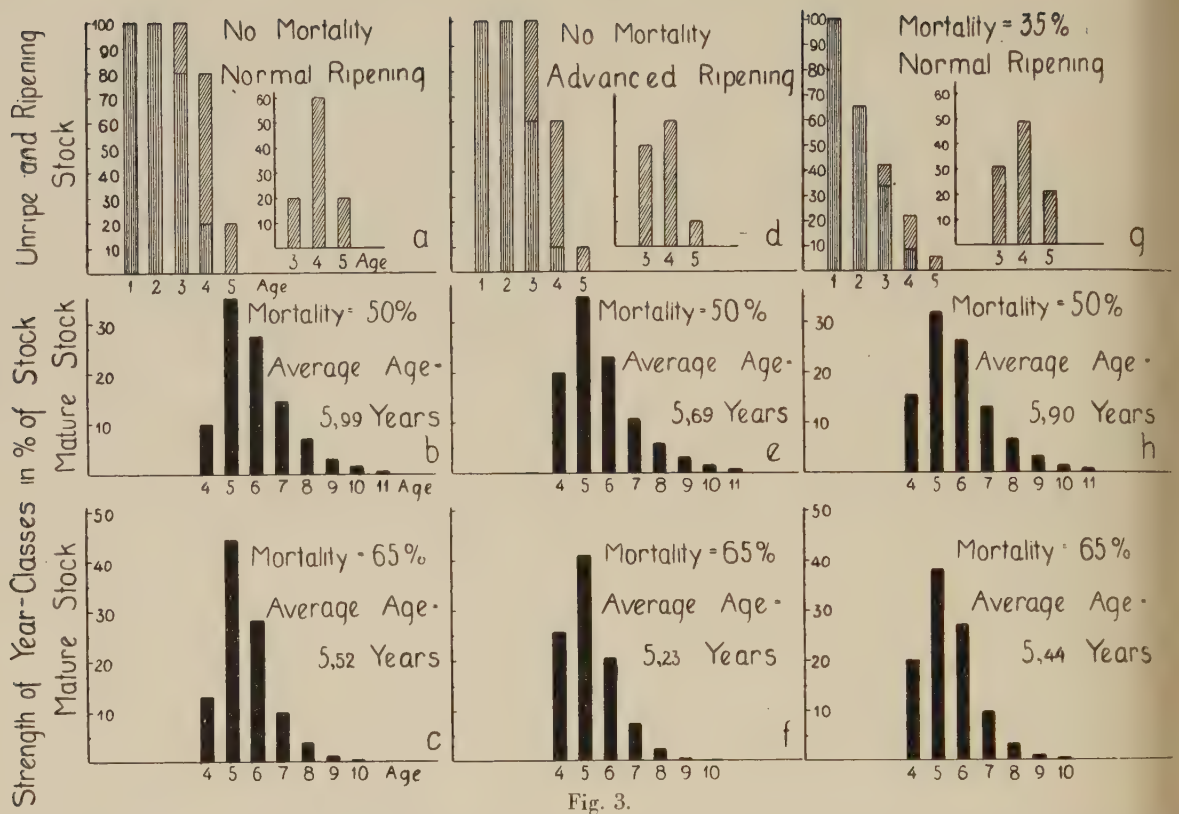


Fig. 3.

5·69 years or 5·23 years respectively. An increase in the mortality of the immature stock also has an influence on the mean age of the sexually mature stock, in as much as it operates in the same manner as an accelerated sexual maturation (Fig. 3g).

If, now, we suppose the mortality of the immature stock to be 35 %, instead of 0 %, then the effect on the mature stock would be a reduction of the mean age to 5·90 or 5·44 respectively.

The reduction in the mean age of the year-classes of the "skrei" has already been demonstrated (Figs. 1 and 2), and we may now discuss this fact in the light of the above-mentioned examples. Let us first consider the changes in the mortality of the Arcto-Norwegian stock of cod, in so far as they are shown by the statistical records of the fishery.

The most important fisheries on this stock of cod are those carried on by the Norwegians, Germans, English, and Russians. Whereas the Norwegian fishery on the stock is procured by means of lines and nets and is comparatively steady from year to year, that of the other nations referred to is mainly a trawl fishery, and the toll taken is therefore of a far more variable nature.

If we now consider the first-mentioned possible cause of the reduction of the mean age, namely, an increased mortality of the "skrei" as such, it is the Norwegian Lofot fishery and the trawling off the north-west Norwegian coast to which we must devote attention.

The Norwegian catch of "skrei" in Lofoten has shown a decline during the period 1932—1936, and this decline has nothing to do with the number of fishermen employed in the fishery.

Year.	Number of fishermen.	Quantity of "skrei" fished.
1932	26,608	105,101 tons
1933	31,905	80,695 „
1934	28,336	87,166 „
1935	28,772	55,098 „
1936	25,043	52,766 „
1937	23,589	82,493 „

On the other hand both the German and English shares in the "skrei" fishery have increased considerably during this period, their landings have more than balanced the reduction in the case of Norway.

German trawling on the "skrei" grounds has developed enormously. Whereas trawling on the banks off Lofoten, Vesterålen and Troms used to be mainly of a subsidiary nature in 1934 regular fishing was started in this area, and from the same year the north-west Norwegian coast became a separate area in the German fishery statistics.

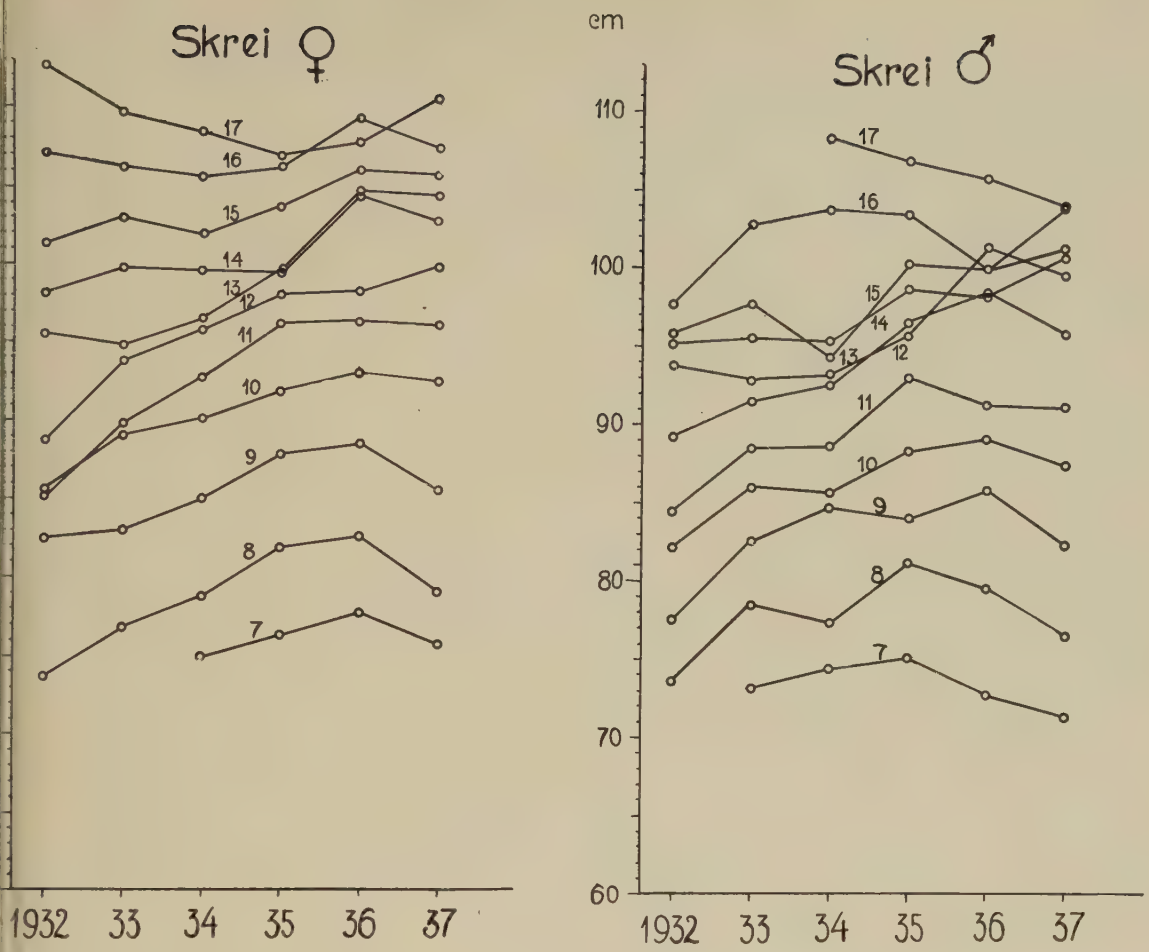


Fig. 4.

cording to records the following voyages nade to these grounds by German and English rs: —

Year.	German trawlers	English Trawlers
1934	190	66
1935	about 500	133
1936	730	193
irst half of 1937	about 900	

1936 the German and English trawlers er fished as much as the Norwegian Lofoten nen, and according to the provisional figures ıave probably fished more in 1937.

›art from a possible reduction of the Nor- n yield of "skrei" by foreign trawling, we also regard this new fishery for the "skrei" additional levy on the stock, and it does not r unreasonable to assume that this extra toll een a contributory cause of the reduction of ean age of the "skrei".

The "loddetorsk" also appears to have been subjected to more intensive fishing in recent years and, particularly on the part of the English and Russians, foreign participation in the fishery of the immature part of the Arcto-Norwegian stock of cod has increased.

Reckoning from 1929 England has increased her trawling voyages to the Barents Sea, Bear Island, and Spitsbergen from 600 to 1660 in 1936, and Russian landings from trawlers have risen from 20,000 tons in 1929 to 60,000 tons in 1935. German trawling, on the other hand, has remained steady during this period, between 600 and 800 voyages per annum, nor has the Norwegian fishery undergone any essential change in magnitude. The greatest absolute increase in the catch of "loddetorsk" falls to England and Russia and the increase represents a total weight of between 100 and 150 million kilogrammes reckoning from 1929.

An increase in the levy on the "loddetorsk" must therefore also be urged as a possible contributory cause of the reduction of the mean age of the "skrei".

The third cause indicated of a reduction in mean age of "skrei" was accelerated sexual maturation. There is one circumstance in particular which indicates that sexual maturation has in fact been accelerated. The degree of correlation between the age of the year-classes and their average length has, as far as the author is aware, been regarded as comparatively constant for particular areas. Comparison between various areas has made it possible to establish a difference in growth-rate in the same species, and in many cases also to explain this as a consequence of the density of population in the different areas. On the other hand, no investigation of the growth-rate of the year-classes within the s a m e area, which would enable an estimate to be made of the changes in the living conditions of the different and successive year-classes, has, as far as the author knows, ever been published.

If we examine the average lengths of the different year-classes on the basis of age analysis and length measurements, we find that, for the six years for which material is at our disposal, these have undergone very great changes. The average lengths for fish of the same age from the landings in different years have been plotted in Fig. 4 and joined by lines, and the diagram shows distinctly that the year-classes in the period 1932—36 have had a continually increasing average length. It is not, however, the annual replenishment of the "s k r ei" stock which has been increased to this degree. It is to be seen that the increase is most apparent among the youngest fish which have just become "skrei". Consequently it is among the "loddetorsk" that a very considerable increase in growth has taken place. An impression of the extent of this change in growth is obtained when the mean value of the average lengths of the different age-groups (8—13 years) in the landings of the respective years is illustrated as in Fig. 5. Fish of the same mean age were about 9 cm. longer in 1936 than they were in 1932.

The reduction of the mean age of the "skrei" might, as mentioned above, be due to accelerated sexual maturation and t h i s i n c r e a s e i n g r o w t h-r a t e may quite conceivably be the cause of the earlier maturation. Even if there is no direct causal connexion between length attained and the inception of sexual maturity, it may also quite conceivably be the case that the same circumstances which have conditioned a more rapid growth have also influenced the course of sexual maturation.

We are undoubtedly here confronted with great changes in the composition of a fish stock, i m-p l y i n g g r e a t s e n s i t i v e n e s s t o e x t e r-n a l f a c t o r s. These changes not only have a great bearing on our conception of the physiological fluctuations of the stock, but concern also its quantitative fluctuations through displacements of the proportion of recruitment to mortality.

The cause of this increased growth-rate need

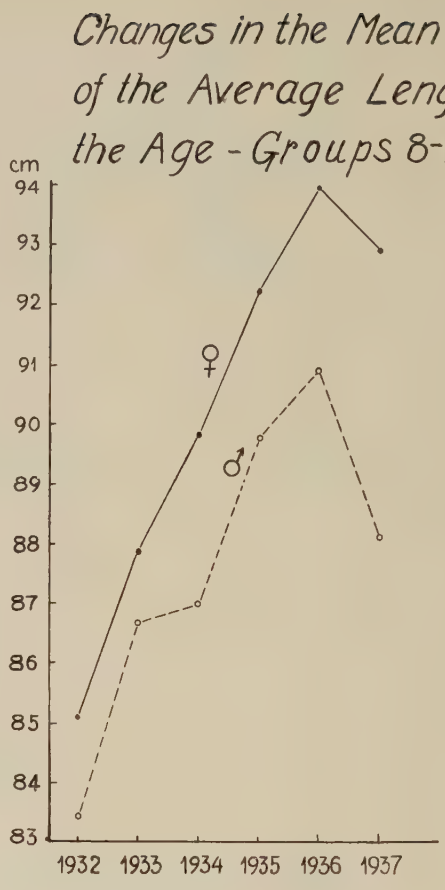


Fig. 5.

not be discussed now, but it must evidently be sought in changes in the meteorological and hydrographical conditions in the Barents Sea.

In three previous publications[1]) the author has reported the discovery of the particularly small outer zones in the otoliths of the "skrei" and, by interpreting them as annual rings acquired after the fish has become sexually mature, he has indicated their importance as a means of determining recruitment and mortality of the "skrei" stock. In this connexion it may be mentioned that the results which have been arrived at by interpreting and treating the narrow outer zones as spawning zones are in full accord with the facts we have here referred; moreover, it is along these lines also that we must look for accelerated sexual maturation and increased mortality in the case of the mature stock as causes of the reduction of the mean age.

1) The Otoliths of the Cod. Fiskeridir. Skr., Vol. IV, No. 3.

The Cod-Otolith as a Guide to Race, Sexual Development and Mortality. Rapp. et Proc.-Verb. Vol. LXXXVIII, 1934.

The Spawning Zone in Cod Otoliths and Prognosis of Stock. Fiskeridir. Skr., Vol. IV, No. 11.

7

SUR QUELQUES PROBLÈMES BIOLOGIQUES LIÉS A L'ÉTUDE DE LA CROISSANCE DES POISSONS.

PAR

L. FAGE ET A. VEILLET,

Institut Océanographique, Paris.

C'EST en réponse au voeu exprimé l'an dernier par le Conseil International pour l'Exploration de la Mer que nous voulons rappeler brièvement dans cette note les conclusions qui se dégagent des études entreprises sur la croissance de quelques espèces de poissons comestibles dont la pêche est activement pratiquée dans le "Secteur Atlantique": essayer de préciser la nature des facteurs susceptibles de modifier la vitesse de ce phénomène et indiquer le rôle de ces modifications dans l'acquisition des caractères somatiques utilisés pour la distinction des races. Nous retiendrons spécialement les travaux publiés sur la **Cardine** (*Lepidorhombus megastoma* Donov.) le **Rouget** (*Mullus barbatus* L.), le **Tacaud** (*Gadus luscus* L.), le **Merlu** (*Merlucius merluccius* L.); la **Sardine** et l'**Anchois.**

Tous ces travaux — comme ceux poursuivis sur d'autres espèces fréquentant les "secteurs" voisins — mènent à la conclusion que la vitesse de la croissance et les rapports de l'accroissement des différentes parties du corps à la longueur totale peuvent varier pour une même espèce avec l'âge, le sexe et la localisation géographique des individus.

P. Chevey[1]) pour le **tacaud**, J. Furnestin[2]) pour la **cardine** ont établi que les femelles croissent plus rapidement que les mâles et arrivent plus tôt à maturité dans le Golfe de Gascogne que dans la Mer du Nord ou la Manche, où on leur trouve une moyenne vertébrale supérieure à celle des individus de l'Atlantique.

Des précisions plus grandes nous sont fournies sur le **merlu** et sur le **rouget**. Nous savons par les travaux de G. Belloc[3]) que, dans toutes les régions fréquentées par le **merlu**, les femelles croissent beaucoup plus rapidement que les mâles, et que, dans l'Atlantique, la croissance est d'autant plus rapide et la moyenne vertébrale d'autant plus faible qu'il s'agit de populations plus méridionales: le merlu, à huit ans, mesure 65 cm. en Irlande, 71 cm. dans le Golfe de Gascogne et 78 cm. au Maroc. Mais, en Méditerranée, il ne mesure a même âge que 30 cm., et nous aurons à recherche les raisons de cette particularité.

Dans ses belles études sur cette espèce, Hickling[4]) précise qu'au S. et à l'W. de l'Irlande le femelles croissent avec la même vitesse que le mâles pendant les trois premières années e qu'ensuite elles prennent l'avantage, qui s'accentu

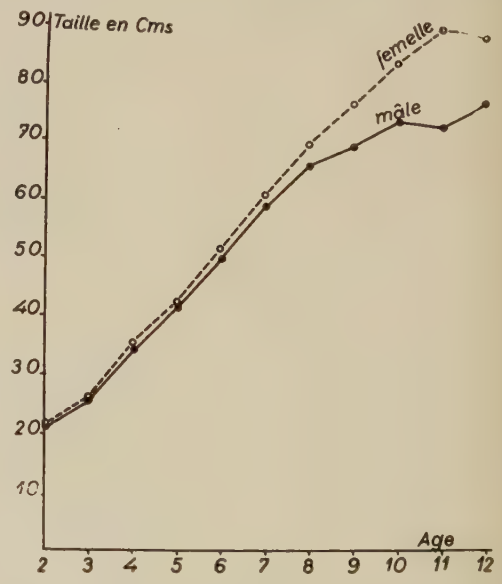


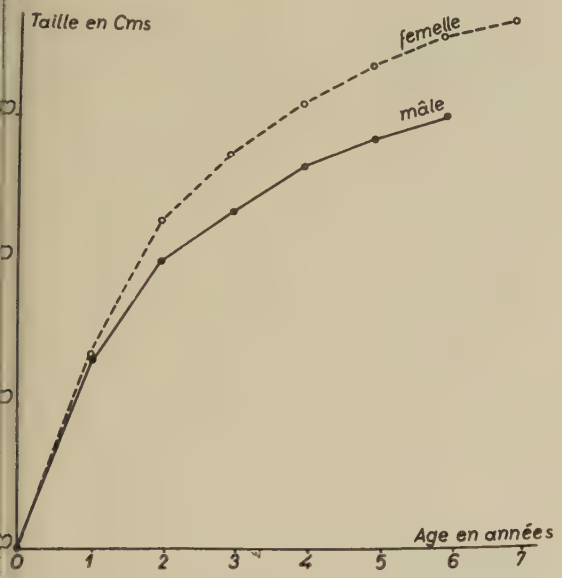
Fig. 1. Vitesse de croissance du Merlu du S. et W. d'Irlande, d'après C. F. Hickling.

progressivement avec l'âge. Or, on sait que le mâles ont leur première maturité sexuelle à troi ans, à une taille de 27 cm. et que les femelles n deviennent mûres pour la première fois qu'à un taille de 70—80 cm., atteinte au cours de leu neuvième année.

Nous voyons déjà apparaître dans ces observa tions l'influence prépondérante de l'apparition d la première maturité sexuelle sur la vitesse de l croissance.

[1]) Rev. Trav. Off. Pêches, II, fasc. 1, 1929.
[2]) *Id.*, VIII, fasc. 2, 1935.
[3]) *Id.*, II, 1929.
[4]) Fish. Investig. Ser. II, XIII, No. 2, 1933.

Avec le **rouget**, nous allons constater que ces férentes modalités dans la croissance influent les proportions du corps. Desbrosses[5]), s une étude très minutieuse de cette espèce, a ntré en effet que, au cours de sa croissance, le get passe par deux stades critiques. Le premier place au moment où le jeune alevin, long de à 13 cm., ayant abandonné la vie pélagique, nt de gagner la côte. Avant ce stade, dans la e comprenant la région antérieure du tronc et partie operculaire de la tête, la croissance en uteur était la plus rapide; mais, bientôt, ce centre croissance se dédouble en un premier situé dans région préorbitaire et un deuxième reporté en ière des pectorales: le corps augmente de hauteur la longueur relative de la tête diminue.



. 2. Vitesse de croissance du Rouget de l'Atlantique, d'après les données de Desbrosses.

Or, cette première crise qui affecte tous les lividus et se produit durant le quatrième et le nquième mois, coïncide avec le début du veloppement des glandes génitales chez les eux sexes. La seconde crise n'affecte e les femelles; elle se produit à l'âge de u ans quand celles-ci, longues de 19·5 à 22 cm., viennent mûres pour la première fois: la crois- nce est accélérée dans les centres préexistants, le rps s'accroît en épaisseur, la région préorbitaire le tronc grandissent très vite et la région post- ale très lentement.

Chez les mâles, au contraire, qui atteignent plus écocement (18—20·4 cm.) leur première maturité sexuelle, cette seconde crise ne se manifeste point et la croissance se continue suivant le mode initial; on constate simplement chez eux, à partir de ce moment, un ralentissement considérable de la croissance en longueur et de l'accroissement en poids. Il est intéressant de noter, en passant, que les mâles de l'Atlantique tendent ainsi vers des proportions (museau court, espace interorbitaire inférieur au diamètre de l'oeil) qui les rapprochent du rouget de la Méditerranée (*Mullus barbatus* forma typica).

Ces changements successifs dans le mode de croissance, qui se traduisent par des proportions différentes à chaque âge envisagé, sont ainsi manifestement en relation avec le développement des gonades. Ils montrent que les hormones sexuelles influent sur la croissance et suivant des modalités propres à chaque sexe.

C'est à des conclusions analogues qu'aboutissent les recherches de Fage[6]) sur les **clupéidés**. Les femelles de **sardine** croissent plus rapidement en longueur que les mâles et ont une tête relativement plus courte. De plus, la vitesse et le mode de croissance — et celà est particulièrement net chez l'anchois — varient non seulement avec l'âge, mais aussi avec la distribution géographique des populations. En effet, les larves de sardine issues d'oeufs pondus à peu près à la même température, en hiver sur les côtes S. et W. d'Espagne et de Portugal, et en été dans la Manche, poursuivent leur développement et leur première croissance dans des eaux dont la température va, dans le premier cas, continuellement en augmentant, et, dans le second, continuellement en diminuant. Le résultat en est que la période initiale de croissance, limitée par l'arrivée du premier hiver, se termine à la taille de 11·6 cm. en moyenne à Cadix, à Sebutal et à Vigo, et seulement à la taille de 6 à 9·5 cm. sur la côte anglaise. Dès la deuxième période, les écarts s'atténuent en raison de l'accélération très nette de la croissance qui se manifeste et se poursuit désormais chez les populations septentrionales, où la taille et le nombre moyen de vertèbres sont sensiblement plus élevés.

Chez l'**anchois**, le mode de croissance est identique pour les populations de la Mer du Nord et celles de la Méditerranée jusqu'au moment de la maturité sexuelle. A ce moment intervient en Méditerranée un ralentissement marqué dans la croissance, ralentissement qui porte principalement sur la partie postanale. Dans la Mer du Nord, au contraire — comme pour les rougets mâles — c'est le mode initial de croissance qui est conservé. Il en résulte que ces deux populations ne se distinguent pas seulement par le nombre élevé de la moyenne vertébrale caractéristique des individus septentrionaux, mais aussi par la longueur de la partie postanale et la brièveté de la tête de ces derniers.

[5]) Rev. Trav. Off. Pêches, IX, 1936.

[6]) Report Dan. Ocean. Exped. II, 1920. *Engraulidae, Clupeidae.*

De ces faits, très brièvement résumés, on peut conclure que:

(1) La vitesse de la croissance est influencée par des facteurs internes dont le plus apparent est le développement des glandes sexuelles, l'activité génitale amenant un ralentissement de la croissance. Il s'agit là d'un phénomène très général constaté non seulement chez les poissons et d'autres vertébrés, mais aussi chez bon nombre d'invertébrés.

(2) Après la puberté, la croissance peut reprendre soit sur le même mode que précédemment (rouget ♂, sardine, anchois de la Mer du Nord) soit sur un mode différent (rouget ♀, anchois de la Méditerranée). Certaines modalités de croissance sont donc en rapport avec le sexe et la localisation géographique des individus.

(3) Les modifications dans la vitesse de croissance ou dans son mode se traduisent par des variations dans les proportions relatives des différentes parties du corps. Il existe ainsi pour une même espèce des variations morphologiques sexuelles et géographiques. Ces dernières sont utilisées pour caractériser les races.

Donc tout facteur susceptible de hâter ou de retarder la première maturité sexuelle aura une influence prédominante sur la croissance. Deux ordres de facteurs sont dans ce cas: les facteurs externes, ou facteurs du milieu, et les facteurs internes.

Parmi les premiers on peut invoquer d'abord tous ceux que l'on sait influer sur la vitesse du développement. Car lorsque nous parlons de vitesse de croissance nous parlons de l'allongement linéaire, phénomène, que non seulement il ne faut pas confondre avec la vitesse du développement mais qui lui est antagoniste: plus le développement est rapide, plus la maturité sexuelle intervient tôt et plus la taille des individus à ce moment est faible et se maintiendra telle par la suite.

Rien n'est plus démonstratif à ce point de vue que ce que révèle l'histoire du merlu dont le mâle a un développement accéléré, puisqu'il est mûr à 3 ans et la femelle seulement à 8 ans, et une croissance beaucoup plus lente que celle de la femelle. Et ne serait-ce pas à un développement particulièrement accéléré et par suite à une maturité précoce que serait due l'existence de la race naine de la Méditerranée? Ne serait-ce pas par ce que le développement de la sardine de la Manche est retardée qu'elle atteint une taille et un âge inconnus en Méditerranée?

La rapidité du développement mérite donc, on le voit, d'entrer en ligne de compte à propos de la croissance. Mais cette question mérite en outre un sérieux examen du fait de ses conséquences morphologiques possibles. En effet, si les proportions du corps sont sous la dépendance de la croissance, certains faits tendent à montrer que les caractères numériques (rayons, vertèbres), encore plus souvent utilisés pour la distinction des races, peuvent être influencés par la vitesse du développement. Nous ne pouvons mie faire à ce propos que de renvoyer à l'exposé suggestif de S. Johnsen[7]) dans lequel facteurs du milieu sont considérés dans leur acti sur la rapidité du développement et sur l'époq plus ou moins précoce où est atteinte la pério critique, celle où les caractères numériques so définitivement fixés. Bornons-nous à indiquer qu bien souvent, plus le développement est accélé plus est faible le nombre de vertèbres. Nous n donnerons qu'un seul exemple: l'anguille d'Euro a un développement larvaire qui dure au moi 2 ans ½, elle possède 111 à 119 vertèbre l'anguille d'Amérique, dont le développement e beaucoup plus rapide, 1 an environ, a seuleme 104—111 vertèbres. L'histoire du développeme de nos pleuronectes fournirait des exemples moins aussi topiques.

Peut-être pourrait-on trouver là une explicatio valable pour de nombreux cas, de ce fait général ment constaté que, dans une même espèce, l populations méridionales ont un nombre vertèbres inférieur aux populations septentrionale — à la condition que puisse être précisé à qu stade du développement se place, dans chaque ca la période critique où les caractères numérique sont définitivement acquis.

Quoi qu'il en soit, si nous avons tenu à cite l'anguille et les pleuronectes c'est qu'il résulte de travaux de E. Murr et A. Sklawer[8]) que, che l'une comme chez les autres, la thyroïde sembl jouer un rôle important dans leur métamorphos Au surplus, l'action sur la croissance des hormone sexuelles est, on l'a vu, évidente. Les facteu externes ne sont donc pas les seuls susceptible d'influer sur la rapidité du développement.

L'action des facteurs internes, et spécialemer des hormones, sur le développement et la croissanc est certaine. Mais, nous touchons là à des questio encore fort peu étudiées chez les poissons et qu méritent cependant un examen attentif. N'a-t-on pa donné récemment[9]) de bonnes raisons de croire qu les deux sous-espèces ou variétés du roug mediterranéen (*Mullus barbatus* et *M. surmuletus* ne sont que des variantes endocrines d'une mêm espèce?

On voit combien la croissance des poissons e un problème complexe qui doit être envisagé sou les angles les plus divers; mais l'on voit aussi qu sa solution peut largement contribuer à éclairer c autre grand problème qui depuis longtemps pr occupe, à juste titre, les savants du Conseil Inte national: le problème des races.

Nous espérons, que des recherches actuellemer en cours nous permettront d'apporter notre co tribution à cette oeuvre.

---

[7]) Bergens Museum Årbok 1936, No. 4.

[8]) Zeitschr. vergl. Physiol. VII, 1928 et Forsch. Fortschr., Berlin, VI, 1930.

[9]) E. Remotti: Boll. Musei Zool. R. Univers. Genov XIII, 1933. No. 69.

8

ON THE GROWTH OF THE COD WITHIN THE TRANSITION AREA.

BY

ERIK M. POULSEN.

THE growth of the cod in the Transition Area has been dealt with in the following papers.

(1) Petersen, C. G. Joh., 1902: The Biology of the Cod in the Danish Seas. Rep. Dan. Biol. Stat., XI.

(2) Strodtmann, S., 1918: Weitere Untersuchungen über Ostseefische, III. Ber. D. Wiss. Meeresunters. N.F., Abt. Helgoland, XIV, 1.

(3) Strubberg, A. C., 1922: Marking Experiments with Cod in Danish waters 1905—1913. Medd. Komm. Havunders., Ser. Fiskeri, VII, 1.

(4) Poulsen, Erik M., 1931: Biological Investigations upon the Cod in Danish Waters. Medd. Komm. Danmarks Fiskeri- og Havunders., Ser. Fiskeri, IX, 1.

In the Transition Area spawning takes place during the first half of the year; in the Skagerak however, it is possible that the cod begins spawning as early as in the preceding December. In spite of this the "birthday" of the cod is in all cases fixed as April 1st, and the cod is reckoned as 0-group in the year when it has its first summer growth season as bottom stage; thus a cod born in December is recorded as belonging to the year-class of the following year. In the Skagerak and the Kattegat the main spawning season is February —March, in the Belt Sea March—April, and in the western Baltic April—May. In the central Baltic (east of Bornholm) spawning takes place in June mainly.

The newly hatched cod larvae are 4 mm. in length. During the first growth season (until November) the young cod attains the following lengths in the verious areas (4):—

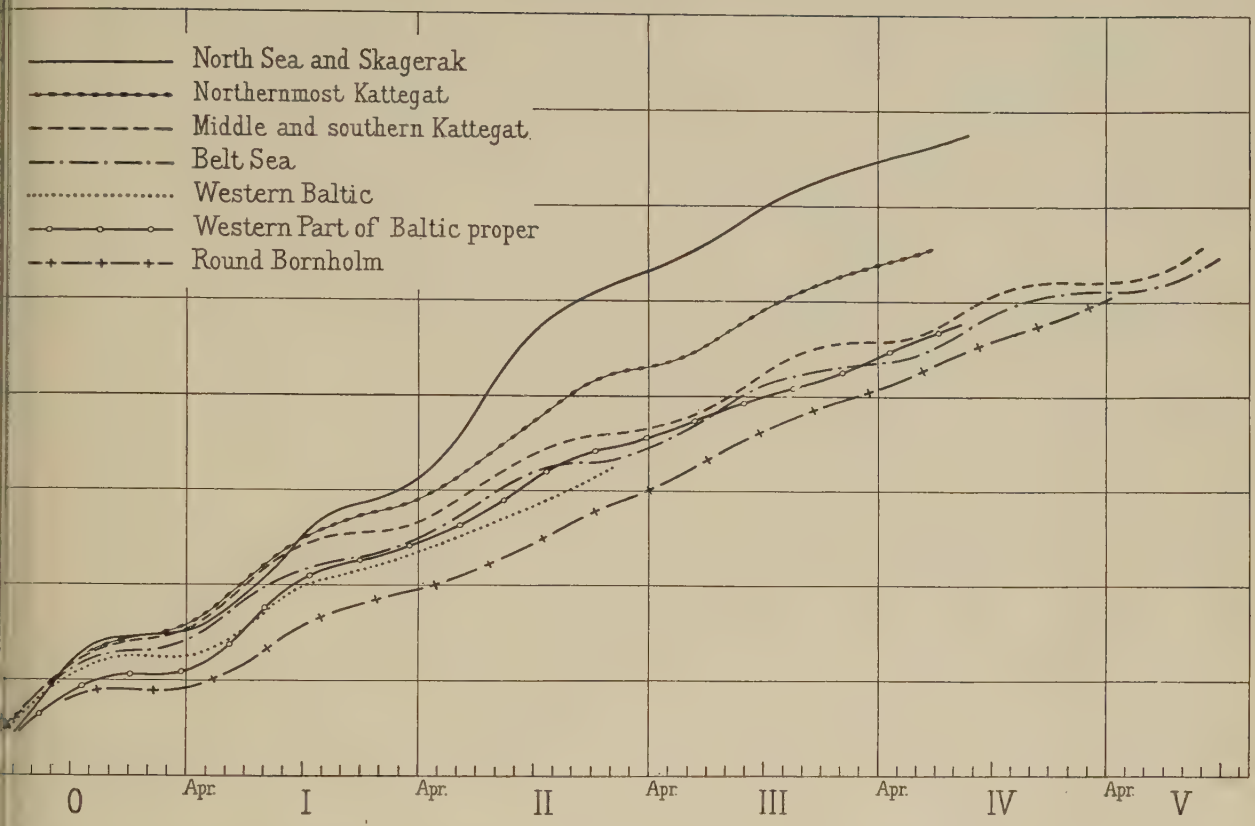
Skagerak	Kattegat	Belt Sea	W. Baltic	Baltic proper
15·5 cm.	14 cm.	13 cm.	ca. 12 cm.	ca. 8—11 cm.

Thus the 0-group reaches a greater mean length in the Skagerak than in the Baltic. However this does not necessarily mean that the growth-rate is higher in the former than in the latter area; it may be caused by the fact that the growth season is longer in the Skagerak, where the spawning takes place early in the year, than in the Baltic, where the cod spawns about 2—3 months later.

The growth of the cod during its following life years is seen from Fig. 1 (after Erik M. Poulsen, 1931). It is obvious that the growth-rate gradually diminishes from the Skagerak through the Kattegat and the Belts into the Baltic. The lesser growth-rate in the southern part of the area is to a certain degree caused by the fact that maturity is reached at an earlier age in these waters than in the northern part of the area: In the northern part about 25 % of the II-group become mature at the end of the year, while on the other hand in the southern part no less than 75 %. From Fig. 1 it is seen that accordingly in the northern part the II-group still has a high growth-rate, but in the southern part a considerably slower growth-rate. On the whole the number of seasons with rapid growth are fewer in the south than in the north.

The different age at first maturity is however not sufficient to explain the observed differences in growth, in as much as the I-group also grows more slowly in the south than in the north, though only very few of its individuals become mature. As the maturing of the sex organs thus cannot account for the varying growth-rate, other factors must play a part. On the basis of our present knowledge it can hardly be decided what these other factors are. The factors may be external: worse conditions of food, decreasing salinity, low winter temperatures, or internal factors connected with racial features. In this respect it should however be remembered that for another species of fish, the plaice, the rate of growth has turned out not to be due to racial characteristics but to depend on the feeding conditions.

There seems to be some evidence to show that the rich year-classes grow more slowly than the poor year-classes:—



N. of Læsø, 0-Group
h 1929 year-class, 13/9: 9·9 cm. (32 fish).
r 1922 year-class, 15/9: 12·1 cm. (35 fish).

The Sound, I-Group
1 1923 year-class, 31/7: 19·9 cm. (18 fish).
r 1928 year-class, 29/7: 22·6 cm. (40 fish).

Northern Belt Sea
1 1923 year-class, 27/8—5/9: 18·5 cm. (40 fish).
r 1918 year-class, 14/8—17/9: 24·2 cm. (45 fish).

These samples[1]) tend to show that the 0-group I-group of the rich year-classes have a somewhat slower rate of growth than the poor ones.

[1]) All caught by the same gear, the Eeltog.

But owing to the very varying conditions under which the 0-group grows in the Transition Area, the material is too small to show anything definite as to the different growth of the rich and the poor year-classes.

The individual growth-rate is dealt with by Strubberg (1922) on the basis of marking experiments, his main result regarding growth being that the strongest growth-rate is found in the Skagerak and in the Little Belt (12 cm. on the average for all species in the year after the marking), whereas in the Kattegat (7—9 cm.) and elsewhere in the Belt Sea (mature 4—5 cm., immature about 12 cm.) the rate of growth is generally slower.

9

ON THE GROWTH OF THE BALTIC PLAICE.

BY

ERIK M. POULSEN.

IN the following, "Baltic plaice" is to be understood as plaice from the Baltic proper, i.e., the waters south of the Sound and east of the line Gedser—Darss.

The plaice of these waters belong to a separate race or group of races characterized by a lower number of anal fin rays and also by a lower number of vertebrae than plaice from other waters. It was formerly assumed that a low growth-rate of a certain value was a character of this race too. Recent investigations, however, have shown that under favourable conditions the Baltic plaice is able to grow as fast as the North Sea plaice.

The growth and growth-rate of the Baltic plaice have been dealt with in recent years in the following papers.

C. G. Joh. Petersen: The influence of fishing upon the stock of the plaice in the Baltic during recent years. Rep. Dan. Biol. Stat., 31, 1925.

S. Strodtmann und Langhammer: Untersuchungen über die Scholle in der westlichen Ostsee. Ber. deutsch. Wiss. Komm. f. Mf., N.F., Bd. I, 1925.

A. R. Molander: Undersökningar över Rödspotta etc. i södra Östersjön. Svensk. hydr.-biol. Komm. Skr., N.S., Biologi, I, 1925.

A. R. Molander: Recent researches into the fish population of the southern Baltic. Ibid., 1926.

R. Kändler: Erneuerung und Nutzung des Schollen- und Flunderbestandes im Gebiet der Oder Bank. Ber. deutsch. wiss. Komm. f. Mf., N.F., Bd. VI, 1, 1931.

S. Strodtmann: Das Wachstum der Schollen in der Ostsee. Ibid., Bd. VII, 1935.

For the waters east of Falster, Petersen (1925) compares his recent material with Reibisch's from 1908—09; the main results of this comparison are shown in the following table, the number of fish being shown in brackets:—

	Aug. 1908—Oct. 1909	Aug. 1921 and 1922	July—Aug. 1924
II-group	—	14·5 cm. (96)	—
III-group	15·2 cm. (31)	17·4 cm. (50)	26·7 cm. (22)
IV-group	18·4 cm. (32)	—	26·4 cm. (43)
V-group	19·3 cm. (51)	—	27·3 cm. (74)

As Petersen states, it is evident that 1908—09 growth was exceedingly slow compar with the growth in 1924. Petersen furth shows that the density of the plaice population h diminished greatly in the intervening years and draws the obviously correct conclusion that t increased growth-rate is due to better feeding co ditions caused by diminished density of the stoc

Strodtmann and Langhammer al published in 1925 some investigations regardi the growth of the Baltic plaice. Investigations the area east of Falster were carried out in sprin 1922, and the following observations of age a length (cm.) were made:—

Age-group	III	IV	V	VI	VII
cm. ♂	22·6	22·9	23·0	23·0	22·9
cm. ♀	23·7	23·7	24·7	27·2	28·6

In this case no growth was observed at all f the males from the III- to the VII-group, where the length difference for the females was 5 c Comparing this growth-rate with the growth-ra found by A. C. Johansen in 1907—08 t authors arrive at the conclusion that a conside able rise in the growth-rate has taken pla between 1908 and 1922, especially amongst t younger age-groups.

In May 1928 the Danish Biological Stati examined 242 plaice from the area east of Falste In the following table the results of this inves gation are compared with the previous age analyse the table also gives the lengths (cm.) of t 0-group as it appears from the Danish coast fishing experiments with Johansen's young-plai trawl in recent years:—

(see page 61, top)

Age-Group	0	I	II	III	IV	V	VI	VII
rch 1907 (A. C. Johansen)	4·7	11·4	15·0	17·6	—	—	—	—
g. 1908 — Oct. 1909 (Reibisch)	—	—	—	15·2	18·4	19·3	—	—
ring 1922 (Strodtmann u. Langhammer)	—	—	—	23·1	23·3	23·8	25·1	25·8
y—Aug. 1924 (Petersen)	—	—	—	25·8	28·5	29·2	32·6	36·3
y 1928 (Dan. Biol. Stat.)	5·5	—	—	—	—	—	—	—
g.—Sept. 1930—37 (Dan. Biol. Stat.)	—	—	—	—	—	—	—	—

On comparing these figures, it becomes clear t the increase in length of the various age-groups very marked. From 1908 until 1928 the mean gths of the III- IV- and V-groups have increased cm. It is also obvious that the rapid growth of younger age-groups had already begun in 1922 1908 the III-group measured 15 cm., in 1922 cm.), whereas in that year there was no corre-ndingly rapid growth-rate among the older age-ups. In 1928, however, the older fish were also wing rapidly, the difference in length between III- and the VII-groups being then 10·5 cm. ainst only 2·7 cm. in 1922.

The thinning out of the stock of plaice in the ters east of Falster has thus resulted in a marked crease in the growth-rate first of the younger e-groups and later of the older age-groups too. e growth-rate is accordingly not governed by ernal factors only, but by feeding conditions as ll. Here, then, the growth-rate is not a racial aracter but is the stamp of the external condi-ns upon the individuals of the stock; the growth-e is a phaenotypic, not a genotypic character.

During the last 8 years we have had in the area st of Falster one especially rich year-class, viz., e 1934 year-class, whereas all the other year-sses have been more or less poor. Comparing e growth-rate (in the 0-group) of this rich year-ss with that of the other year-classes, we get the llowing figures (the material was collected during e Danish coastal investigations): —

Year-classes 1930—33 and 35—37:
mean length of 0-group in Aug.. 5·7 cm. (45 fish)
Year-class 1934:
mean length of 0-group in Sept.. 5·3 cm. (40 fish).
Though the individuals of the rich 1934 year-class were fished about 3 weeks later than those of the other year-classes, they were half a centimetre smaller than these. This observation shows clearly that the rich year-classes grow slower than the poor ones and, therefore, that feeding conditions may influence growth-rate.

For the area Bornholm—Rügen (the Arcona Basin) the growth-rate can be seen from the following figures: —

Group	II	III	IV	V	VI	VII	VIII—X
11 1921 (Strodtmann u. Langhammer)	—	—	—	22·9 (10)	25·8 (30)	24·9 (104)	25·2 (153)
rch 1922 (A. R. Molander)	16·4 (22)	20·6 (23)	22·3 (12)	24·5 (36)	26·5 (31)	26·0 (29)	—
7 1922 (Strodtmann u. Langhammer)	—	22·4 (13)	24·5 (19)	25·4 (25)	25·8 (73)	25·5 (102)	26·7 (209)
$-21/_8$ 1928 (Danish Biol. Stat.)	—	26·4 (44)	29·1 (31)	30·0 (67)	29·2 (10)	34·1 (6)	37·4 (17)

As appears from the figures, there is a considerable rise in the growth-rate from 1922 until 1928, the length of the age-groups being about 6 cm. longer in 1928 than in 1922. The increased growth-rate has resulted in the Danish size-limit of 26 cm. being reached in 1928 by the III-group, whereas it was first reached by the VI-group in 1922.

The following analyses may be tabulated for the Oder Bank area (a coastal area where the young plaice (0-III-group) grow up): —

Group	0	I	II	III
ne 1930 (after Kändler, 1931)	—	7·0 (6)	13·6 (580)	21·1 (217)
pt. 1930 (Mat. from the "Dana")	7·9 (118)	12·4 (93)	17·9 (300)	24·5 (44)
t. 1930 (after Kändler)	6·4 (346)	12·4 (96)	18·9 (720)	23·7 (30)
y 1937 (Dan. Biol. Stat.)	—	—	17·1 (60)	20·7 (197)

The figures from the various investigations agree rather well with one another. As regards the growth-rate of the various year-classes we may state as follows. The investigations show that in the Baltic the 1934 year-class was comparatively rich. It is apparent from the figures that the 1934

year-class (III-group in 1937) had a slower growth-rate than the poor 1927 year-class (III-group in 1930); at the end of July 1937 it had a mean length of only 20·7 cm., against 21·1 cm. at the beginning of June (1st to 6th) 1930.

The lengths of the various age-groups at the end of the growth season are approximately as follows: —

Group	0	I	II	III
Length about	8	13	19	25

As Kändler states, the growth of the young plaice is more rapid in the Oder Bank area than in the southern part of the North Sea off the German coast.

A comparison with the growth of the young plaice in the Horns Reef Area shows the same results: —

Group	0	I	II	III
Horns Reef Area (autumn 1935*))	7	13	16·8	19·6
Oder Bank	8	13	19	25

*) Aage J. C. Jensen: An Investigation of the Stock of Plaice in the Southern Horns Reef Area in the years 1925 and 1927. Medd. Komm. f. Havunders., Ser. Fiskeri, VIII, 6, 1928.

The growth-rate on the feeding grounds is thus somewhat higher for the Baltic plaice than for the North Sea plaice.

The following figures relate to the deeper area of the Baltic north and east of Bornholm where the older age-groups live:—

Years:	Age: 3	4	5	6	7	8
19th June 1919 (Molander, 1925) ...	—	19 (1)	23 (21)	25 (20)	27 (13)	27 (12)
20th March 1922 (Molander, 1925) ..	—	—	25 (3)	27 (8)	27 (11)	30 (11)
Sept.—Oct. 1925 (Molander, 1926) .	—	24 (155)	27 (211)	29 (151)	32 (96)	33 (35)
Aug. 1928 (Dan. Biol. Stat.)	25 (47)	27 (15)	28 (28)	29 (7)	—	—
Jan. 1931 (Dan. Biol. Stat.)	22 (54)	23 (127)	24 (14)	29 (2)	36 (2)	35 (1)

Though the figures are not quite in agreemen with one another, there is on the whole an increas in the growth-rate from 1919 to 1931. This increas of the growth-rate has been dealt with in detai by A. R. Molander (1925 and 1926). He is n doubt right when he says: "If we look for a explanation of the greatly increased growth of th southern Baltic plaice, we shall no doubt find i in the thinning out of the stock caused by fishing whereby a lessening of the struggle for foo resulted".

By means of the observations of age and lengt of the Baltic plaice it has been shown (cf. th papers cited above) that the rate of growth is no a racial character and is thus not bound up wit the internal condition of the individuals. The rat of growth is governed by external conditions, an as the investigations showed that the rise in th growth-rate occurred simultaneously with a thin ning out of the stock, there is every reason t suppose that the growth-rate is governed in th main by feeding conditions. This supposition i further supported by the fact that in several case it has been established that the growth-rate of th rich year-classes is slower than that of the poo ones.

Nevertheless, to a certain degree the growth-rat must be assumed to be determined by interna factors as far as each species or race has its own range of possibilities of growth-rate, but within this range the growth-rate is primarily governed by feeding conditions.

10

GROWTH OF COD IN THE NORTH SEA AND USE OF THE INFORMATION.

BY

MICHAEL GRAHAM.

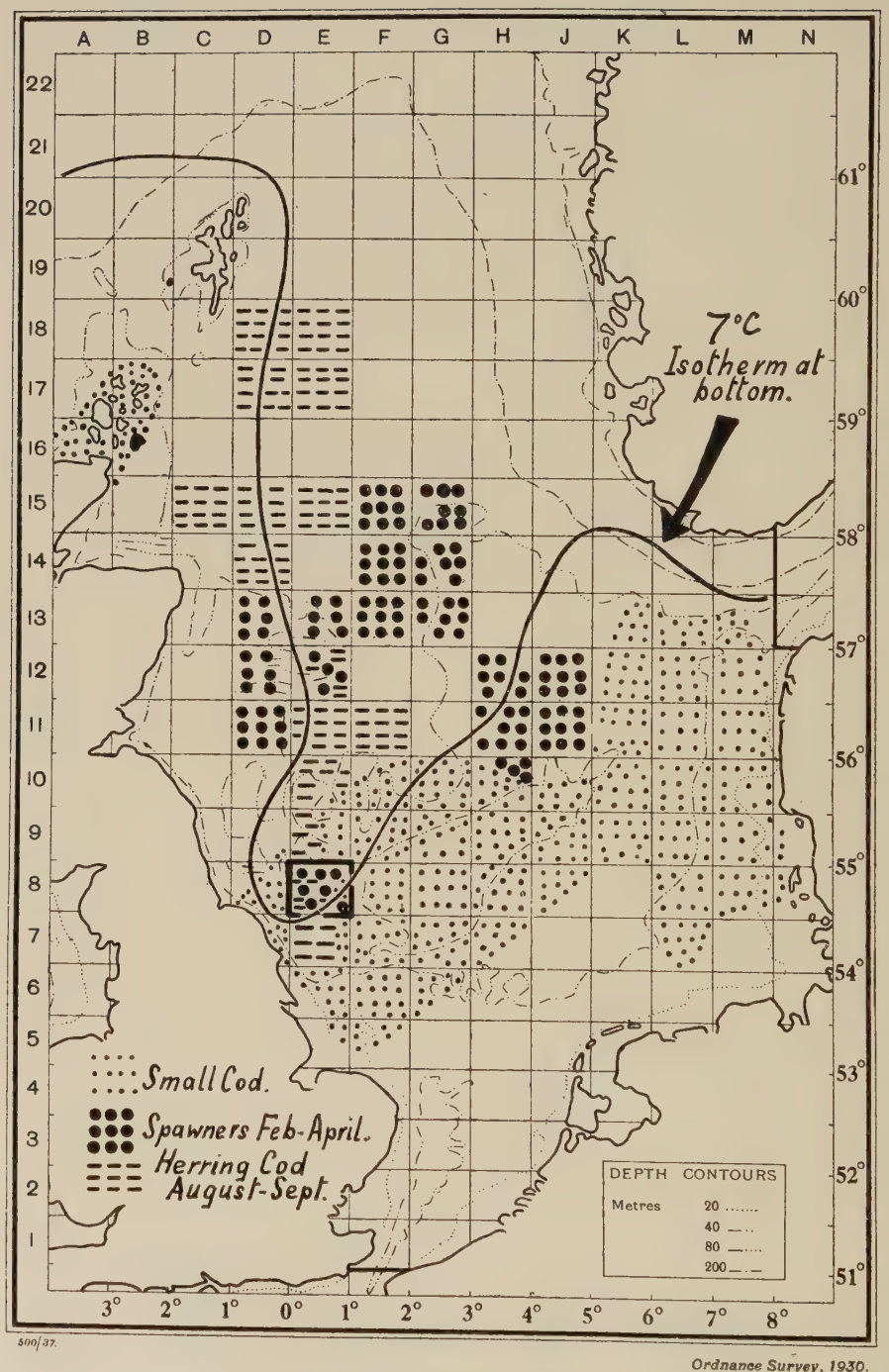

A B C D E F G H J K L M N
22 21 20 19 18 17 16 15 14 13 12 11 10 9 8 7 6 5 4 3 2 1
61° 60° 59° 58° 57° 56° 55° 54° 53° 52° 51°
3° 2° 1° 0° 1° 2° 3° 4° 5° 6° 7° 8°
7°C
Isotherm at bottom.
Small Cod.
Spawners Feb-April.
Herring Cod
August-Sept.
DEPTH CONTOURS
Metres
20
40
80
200
500/37.
Ordnance Survey, 1930.

Fig. 1

Note. Figures in the calculations on pp. 62—65 are subject to small corrections, too little significant to justify resetting the type. Final figures of the more important results are recorded on p. 66.

Introduction.

At the outset I wish to thank Professor Hjort and Dr. Russell for reading the notes on which this memorandum is based and making luable suggestions.

So far as we know all stages in the life history cod are represented within the North Sea. A neral review of what is known has been published brief form in an earlier paper (Graham 34 b). As an example, we show here in Fig. 1 awning grounds, small cod grounds, and grounds cod feeding on herring. Such information pends, for its comprehensiveness, on statistics of ches with the trawl (Graham *et al.* 1924, c. 4; Graham 1934, pp. 45, 69, 74). Trawl tistics do not show one important feature of the e of the cod, namely dispersal after breeding. May and June the large cod disperse widely to d heavily on animals of the bottom. This is own by statistics of line fishermen (Graham *al.* 1924, Chart. 11; Graham 1934, Fig. 3C). cause the generalisation of all this information by statistics, the description can only refer to the pulation of cod that is sampled by the fishery which the statistics have been used. Thus, if re are cod in areas that are less easy to fish with trawl than others, those cod have made a less ntribution to the generalised statement than have e cod of fair grounds. The same principle applies the study of growth.

Growth up to 2 Years Old, mainly of Pre-Marketable Cod.

The frontispiece of an earlier paper shows how e age of young North Sea cod is read from the ales (Graham and Lumby 1929, Fig. 1). e scale in question was read as being just over o years old. Nothing, however, follows from this e determination. A cod 18 months old may be ly 16 cm. long, weighing less than 100 grammes, ile another cod of the same age from the same mple may be nearly 30 cm. long and weigh out 250 grammes (Graham and Lumby 1929, Fig. 20, p. 50; Russell 1922, p. 75). In 1924—1926 the research vessel "George Bligh" was used repeatedly to take samples of some very small codling that were then to be found on the Inner Herring Trawling Ground. The scales of these fish were all examined and tracings reproduced in Graham and Lumby (1929). This collection was the best, from the point of view of continuity, that is likely to be made for very small North Sea cod. It was published 5 years before the results for the rest of the Southern North Sea. Had there been no further publication than the description of growth on the Inner Herring Trawling Ground, the only information for the North Sea would have been the following:—

Age in months	6	12	18	24	30	36
*) Modal length (cm.)	8½	14	19	20	27	29

Now, in spite of the excellent collection on which this table is based and the great care that was taken in proper interpretation of the scales, these figures are unsuitable as a basis for generalisation for great fisheries in the North Sea, because they show exceptionally slow growth. (The collection was made and used as a check on the method of age determination). The Inner Herring Trawling Ground lies in the northern part of rectangle E. 8 and in rectangle E. 9, which, as is shown in Fig. 1, lies north of the common position of the isotherm of 7 degrees of temperature on the bottom in the summer. This isotherm has been taken as a convenient boundary of the area that suffers a thermocline in summer, which lies to the north and west of the isotherm. Now it was found that the samples of scales of all I-group and II-group cod that were collected from under this thermocline showed a growth similar to that of the Inner Herring Trawling Ground, whereas the samples from the area where there is commonly no thermocline showed faster growth. One or two samples from near the boundary showed intermediate or mixed growth. The difference in growth between the two main areas is considerable. At two years old the slow-

*) Approximate average of determinations of modes in samples. Graham 1934, p. 43.

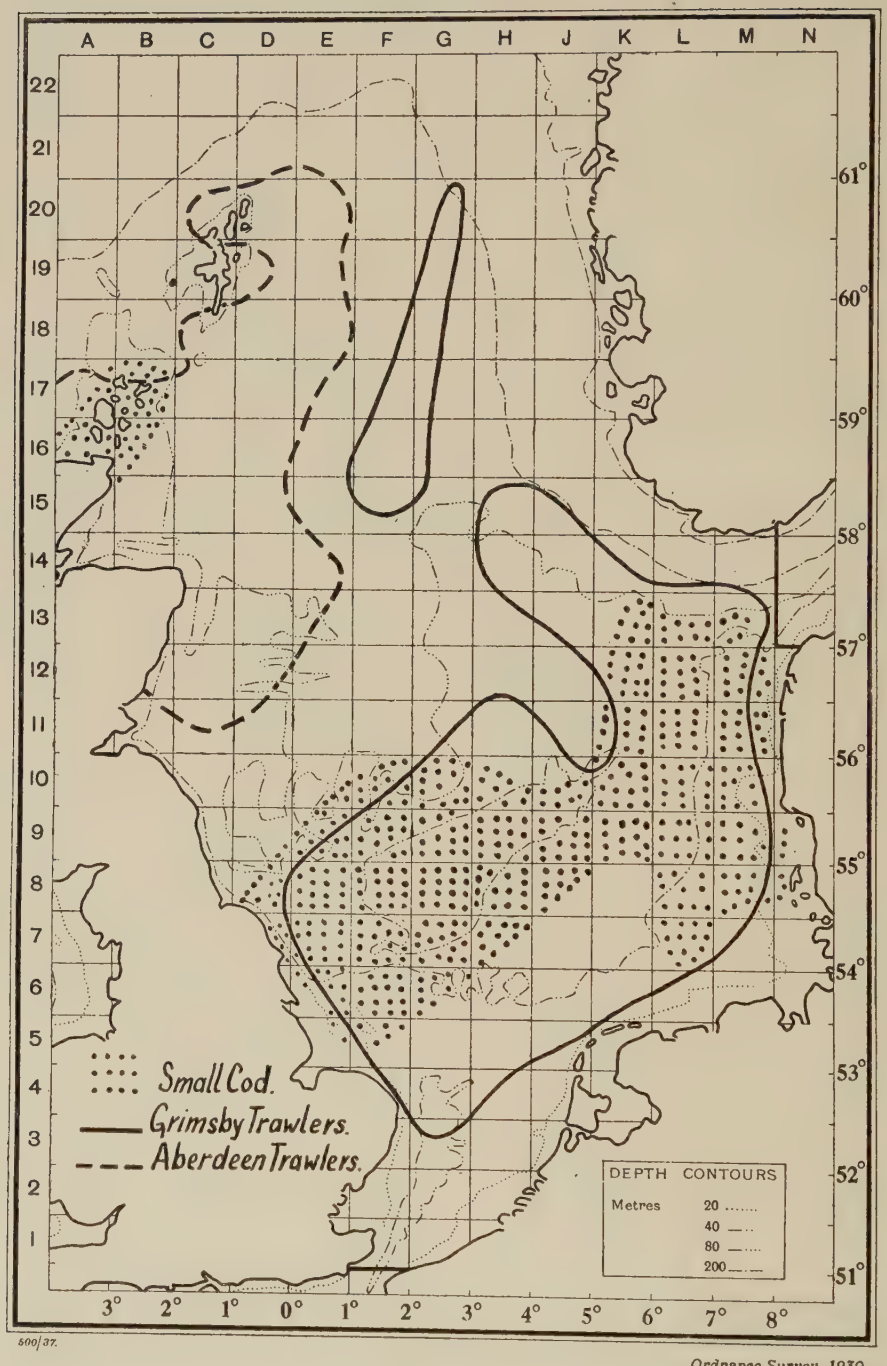

A B C D E F G H J K L M N
22 21 20 19 18 17 16 15 14 13 12 11 10 9 8 7 6 5 4 3 2 1
61° 60° 59° 58° 57° 56° 55° 54° 53° 52° 51°
3° 2° 1° 0° 1° 2° 3° 4° 5° 6° 7° 8°
Small Cod.
Grimsby Trawlers.
Aberdeen Trawlers.
DEPTH CONTOURS
Metres
20
40
80
200
500/37.
Ordnance Survey. 1930.

Fig. 2

wing codling would be about 20 cm. in modal gth, whereas the fast-growing would be 36 cm., ghing about four times as much (G r a h a m 34, pp. 42, 46).

Turning again to Fig. 1, it is observed that the allest statistical category of trawled cod lies nsest in an area that is mainly not subject to a rmocline. It was also known that the fry first ch bottom in an area, which, if anything, lies ll further to the south and east (G r a h a m, a r r u t h e r s and G o o d c h i l d 1926). It was, refore, assumed that the fast growth described plied to the codling that supply the trawl fishery.

rowth within the Trawled Population and "NWG".

So far we have mainly dealt with growth of l before and just after they become marketable. r a h a m 1934, pp. 140, 141). Thereafter the estigation falls into two parts. The first is the ablishment of a table of age at a given length – the population landed by trawlers at Grimsby. iis was founded on measurements made at sea commercial vessels from 1919—1927. The ond is the maintenance of observations of length-tribution of this same population on the market Grimsby. This work is done regularly.

Here we may begin by showing Fig. 2. Had it en possible to add any further lines to Fig. 1, it uld have been better to have put the contours presenting the areas where the greater part of trawling from Grimsby and Aberdeen lies upon g. 1, to show several ways in which the popula-ns of cod landed at the two ports are not the ue. However, it is sufficient to show only the a of Small cod, by way of illustration. It is at e clear that the population of cod landed at imsby will be expected to have a larger pro-rtion of Small among it than the cod landed at erdeen. Similarly it has been shown that the wlers of Lowestoft, Hull, Scarborough, Hartle-ol, North Shields, Granton, and Dundee have aracteristic but overlapping areas and those of great-liners and seiners are different again r a h a m 1934, p. 12). It would require a large ff of observers to sample cod from all these rkets, so no attempt has been made to obtain neralised data for the whole North Sea trawl hery. Instead, inquiry has been restricted to the pulation that is trawled and landed at Grimsby. e steam trawlers at Grimsby landed in 1928 out one third of all the cod that came from the rth Sea, by any fishing method of any country r a h a m 1934, p. 20). The next English port ded less than one quarter of the landing at imsby (G r a h a m 1934, p. 112). There is no estion that the work concerns the largest fishery r cod in the North Sea.

According to the theory expounded by R u s s e l l (1931) the crop or steady yield of a given stock depends, among other things, on the growth-rate. Growth makes a contribution to this crop, recruitment another, whereas natural mortality levies a toll. Calculation based on this reasoning was made in an earlier paper (G r a h a m 1935), where the calculation had a particular form, to demonstrate that there was overfishing. The form was difficult, because only the order of magnitude of the rate of natural mortality could be assumed, not any exact value. For the present purpose this difficulty does not arise. For the calculation, growth is best defined in a certain way. Let N fish in a stock be distributed according to age so that there are:—

at age	$1^1/_2$	$2^1/_2$	$3^1/_2$	.... years
	$n_{1^1/_2}$	$n_{2^1/_2}$	$n_{3^1/_2}$	.... fish
weighing	$w_{1^1/_2}$	$w_{2^1/_2}$	$w_{3^1/_2}$	.... grammes
and let	$g_{1^1/_2}$	$g_{2^1/_2}$	$g_{3^1/_2}$	.... be calculated

according to the formula of perpetual compound interest, that is

$$g_{1^1/_2} = \frac{\log w_2 - \log w_1}{1}$$

and other values of g be calculated similarly.

Now if the stock be in equilibrium with fishing, so that, excluding fluctuations, N and $n_{1^1/_2}\, n_{2^1/_2} \ldots$ have no tendency to increase, decrease, or alter their relative proportion, then the total contribution of growth to the crop, in *grammes per annum* is given by

NWG

which Mr. O t t e s t a d tells me should be written $\Sigma_{nwg.}$

It will be observed that G, the weighted average growth-rate of the fish in the stock, is not the same as G, used by R u s s e l l for the sum of all the increments of weight of the fish in the stock, although we have adopted R u s s e l l's equation as applicable to the processes measured in this way. (G r a h a m 1935).

It is proposed to estimate NWG for different states of equilibrium, of the stock of cod and fishing by the trawlers from Grimsby. The estimates cannot be exact, because they will assume g at any age unchanged. This is thought, however, not to detract from their usefulness, because the changes in NWG are, nevertheless, estimated to be so considerable as to have a high significance.

Although NWG has absolute form, kilogrammes per annum, it will be calculated for a given quantity of stock, that is for the quantity taken in 100 hours fishing of a 1st class steam trawler.

Since G and W are averages, depending on the ratio of values of n at different ages, it is clear how important it is in this calculation to define

the population that is being studied. For example, the stock serving Aberdeen trawlers will contain proportionally more older fish than that of the Grimsby trawlers, as can be seen in Figs. 1 and 2. Consequently neither W nor G can be the same in the two populations, although the distribution of the thermocline and some direct data lead to the conclusion that g is the same.

It is seen that the two parts of the investigation of this section may be redescribed. The first leads to determination of g, at different ages. This has been done, once only. In the second, data are collected continuously for determination of n at different ages, so that current values of NWG shall be available.

It is hoped to redetermine g sufficiently to make sure that there has been no great change since the period 1919—1927 to which the former determination applied. In the meanwhile we rely on the former determination, which may now be described. In cod of these ages in the North Sea age determination by scales has many difficulties. We finally started from the age as given by scales in the younger fish and thereafter proceeded by analysis of statistics of length, of which there was a very fine collection made in the area south and east of the thermocline on board commercial steam trawlers. The analysis was guided by recorded growth of marked fish and supported by the period of successive waves of abundance in the statistics of market categories. (Graham 1934, Sections 3 and 4). The analysis is tabulated on pages 137—139 of Graham (1934). All the observations of the whole period were taken together. For every month except February, for which the data were poor, there is a table showing the length-distribution of each age-group. For example:—

Cod, 2 years old in March. (Graham 1934, p. 137).

Length (5 cm. groups)	25—	30—	35—	40—	45—	50—	Total
No. per mille	21	100	176	122	50	4	473

These frequencies are per 1,000 of the whole stock. The average length is 38·5 cm. A fish of 38·5 cm. would weigh 506 grammes, gutted, according to the average of more than 5,000 determinations (Russell 1922, p. 75). There is no objection to the data for conversion referring to gutted fish, for it is the crop of fish, gutted, in which we are interested. The figure of 506 grammes is the weight of the fish of average length. The average weight, however, is found, in a different manner, from the same data:—

Length (5 cm. groups)..	25—	30—	35—	40—	45—	50—	
Weight (grammes)	183	302	469	680	933	1,262	
Frequency	21	100	176	122	50	4	473
Products	3,843	30,200	82,544	82,960	46,650	5,048	251,245

Dividing the last total by 473, the number of fish the average weight works out at 531 gramme Similarly, the average weight of a 3-year-old co is 1,461 grammes. The determination of g is the as follows:—

Napier's log 1,461 = 7·2869
Napier's log 531 = 6·2748
1·0121 say 1·01

Continuing in the same way, we obtain th following series of figures. These all apply at th half years of age, i.e., in September.

Age, Exactly.

	Years					
	1½	2½	3½	4½	5½	6½
g	1·89	1·01	0·60	0·44	0·39	0·2

(Graham 1935, p. 268)

This first part presented us with figures for that have been used ever since, and also with table of conversion from length to age. This con version table is used in the second part of the study to estimate the age composition, or distribution o n, from statistics of the length-distribution of the landings at Grimsby. These statistics are collected regularly and it may not be out of place to describe briefly how they are obtained. It is thought tha such statistics are best if completely comprehensive that is, refer to all the British 1st class steam trawlers that land their own catch at Grimsby from the North Sea. Referring first to the work on the market, the collectors of statistics keep special records of the quantities of each of the six trade sub-categories of cod that are landed. Two measurers do their best, amongst other duties, to measure 400 fish from each of the trade sub-categories every month.

These records of measurements of fish in each market sub-category are posted to Lowestoft monthly. The frequencies are arranged in 5 cm groups. The weight of the fish that were measured in each sub-category is calculated, using average weights for 5 cm. groups from Russell's table (1922, p. 75). The weight of each sub-category

ed (in cwts.) is supplied separately each month
n Grimsby, and the ratios of these weights to
e of the measured samples are the factors by
h the length-frequency distribution tables are
iplied, giving estimated length-distribution of
landings for each sub-category. Addition of
hese gives number of cod in each length-group
ed during the year.

It is laid down in the work that observers
ld not follow blindly the designations of
els that are given by the trade, but should
ntain in their own minds a standard that they
in naming in the records, either measurements
uantities. There are two measurers, who also
rd some quantities, and three or four other
rders of quantities; so this standard, in so far
t attempts to correct the vagaries of market
tice, which is fortunately only in a small part
he work, has to be common to the minds of
-a-dozen people.

The alternative is to have the fish measured at
before any sorting takes place, as was the
tice from 1921—1930, when only a little time
spent by measurers on the market. The records
, however, found to be quite useless for
nating the length-distribution of the catch of
in any particular year. Two measurers could only, that way, work one vessel at a time, sampling about 30 catches per annum and the variation from voyage to voyage rendered such small sampling inadequate. The same two measurers, with the collection of quantities, now sample the whole of the landing. Their scope is increased as many times as there are trawlers working in the North Sea from Grimsby, namely about 150 times. Naturally, the precision of the statistics is reduced, but this is less important.

Table I shows the length-distribution of the landings per 100 hours fishing in all years for which it is available, together with the weight of the fish in each length-group. Table II is the conversion table taken from the first part of this investigation and Table III gives figures for *n* ("No.") in 1921—1930 and in subsequent years including1936. We have now the information for calculating NWG, firstly for 1921—1930, secondly for some later period. The first calculation was the basis of the conclusion of an earlier paper (G r a h a m 1935, p. 268) except for one difference that may be discussed. It may have been observed that Tables I and II refer to the whole year. That is to say, there is no time during the year when the census would be found as in these tables, but that they represent averages for the whole calendar

Table I.

COD. (Grimsby)

Number and Weight (Kilograms) of Fish caught per 100 hours fishing, and landed by 1st class Steam Trawlers at Grimsby from the North Sea.

ngth	Average 1921—1930		1931		1932		1933		1934		1935		1936		Average 1931—1936	
	No.	Wt. kg.	No.	Wt. kg.	No.	Wt. kg.	No.	Wt. kg.	No.	Wt. kg.	No.	Wt. kg.	No.	Wt. kg.	No.	Wt. kg.
– ..	2	0	3	0	8	1	4	0	1	0	0	0	1	0	3	0
– ..	58	11	64	12	320	59	102	19	68	12	21	4	57	10	105	19
– ..	144	43	169	51	534	161	519	157	190	57	82	25	182	55	280	84
– ..	140	66	148	70	345	162	518	243	125	58	110	51	160	75	234	110
– ..	110	74	118	80	163	111	356	242	89	61	92	62	102	70	153	104
– ..	82	77	76	71	56	53	163	152	95	89	101	94	60	56	92	86
– ..	68	86	41	52	42	53	77	97	104	131	71	89	33	42	61	77
– ..	53	78	40	60	58	86	66	98	77	114	38	57	30	45	52	77
– ..	36	74	52	108	56	116	64	133	78	160	24	50	27	56	50	104
– ..	31	81	55	144	42	111	57	149	60	157	18	48	22	58	42	111
– ..	26	84	31	101	31	100	32	104	29	96	19	62	16	51	26	86
– ..	14	57	16	66	25	103	22	90	17	68	17	68	10	41	18	73
– ..	12	60	8	42	15	75	15	76	11	56	13	63	8	40	12	59
– ..	11	66	7	40	9	52	12	70	9	56	8	46	8	48	9	52
– ..	13	89	9	61	7	46	9	66	8	59	6	42	8	54	8	55
– ..	10	77	8	61	6	46	6	46	7	58	5	43	5	41	6	49
– ..	6	52	5	40	5	41	4	33	4	39	4	32	4	31	4	36
– ..	2	16	2	16	2	18	2	20	2	20	2	16	1	13	2	17
– ..	0	0	1	6	1	8	1	8	1	8	0	0	1	6	1	6
– ..			0		0	0	0	0	0	0	0	0	0	0	0	0
– ..	0	0									0	0	0	0	0	0
ls ..	818	1,091	853	1,081	1,725	1,402	2,029	1,803	975	1,299	631	852	735	792	1,158	1,205

Table II.

Age-Composition of Cod of given Length-Groups.

The following table of the average age composition of each length-group during 1919—1927 was prepared from Tables 30 and 31 of Graham, 1934, interpolating for the month of February. The numbers in each age-group are expressed as percentages of the number in the length-group.

5 cm. Length-Group	Age-Group 0	I	II	III	IV	V	VI	VII	VIII
	%	%	%	%	%	%	%	%	%
20— ...	11	78	11	—	—	—	—	—	—
25— ...	1	84	15	—	—	—	—	—	—
30— ...	1	75	24	—	—	—	—	—	—
35— ...	—	55	45	—	—	—	—	—	—
40— ...	—	35	65	—	—	—	—	—	—
45— ...	—	15	77	8	—	—	—	—	—
50— ...	—	1	72	27	—	—	—	—	—
55— ...	—	—	43	57	—	—	—	—	—
60— ...	—	—	17	74	9	—	—	—	—
65— ...	—	—	3	62	35	—	—	—	—
70— ...	—	—	—	21	72	7	—	—	—
75— ...	—	—	—	—	65	35	—	—	—
80— ...	—	—	—	—	23	71	6	—	—
85— ...	—	—	—	—	—	64	36	—	—
90— ...	—	—	—	—	—	25	67	8	—
95— ...	—	—	—	—	—	—	75	25	—
100— ...	—	—	—	—	—	—	40	60	—
105— ...	—	—	—	—	—	—	—	100	—

year. In the earlier paper the calculation given in the text referred to the month of September, which is half-way through the year of life of the cod, assumed to start in March. I do not know which is the better procedure, but it is unlikely that either procedure will give misleading results in comparisons, so long as it is used throughout.

The value of NWG is the sum of the *nwg*'s for each age-group. Thus Table III shows 288 I-grc fish per 100 hours fishing, in the period 192 1930. By applying a conversion table to th length-distribution the column "Wt" was obtai showing that these 288 fish were estimated to we altogether 116 kg. This is *nw*. Turning back the figure for $g\ 1\frac{1}{2}$, we find that the contribut to the crop of the growth of the I-group in stock represented by 100 hours fishing of a class trawler of Grimsby is $116 \times 1{\cdot}89$ or 2 kilogrammes per annum. Similar multiplicatic can be made for all the groups for which there a value of *g*. When these are added together th come to 763 kilogrammes per annum. Three co ments may be made here. In the first place th can be called *763 kilogrammes per annum per 2 recruits of the I-group* and of such older recru as may be expected to join up with that numb of I-group recruits. This is an alternative definiti to that involving consideration of fishing tim Secondly, it will be noted that *g* was calculat from instantaneous data, but is here applied average data. Perhaps there is some better proc dure than this. Thirdly, it seems not possible include the contributions of the oldest and younge groups, owing to lack of data of *g*.

To recapitulate:— If the stock of cod was equilibrium with fishing in 1921—1930, the co tribution of growth to the yield was 763 kil grammes per 288 I-group recruits.

Use of the Method to judge whether Fishing should be decreased for better Profit.

We have seen that other things come into t estimate of steady yield, or crop, than grow alone, and it has been decided in an earlier pap (Graham 1935) that the fishing of 1919—19

Table III.

COD. (Grimsby).

Numbers and Weights from Table I arranged according to Age-Groups, assuming that the Age Compositi of any Length-Group is the same as in 1919—1927 (Table II).

Age Group	Average 1921—1930		1931		1932		1933		1934		1935		1936		Average 1931—193	
	No.	Wt. kg.	No.	Wt. kg.	No.	Wt. kg.	No.	Wt. kg.	No.	Wt. kg.	No.	Wt. kg.	No.	Wt. kg.	No.	Wt. kg.
0	1	1	3	1	9	2	7	1	3	0	1	0	3	1	4	
I	288	116	317	125	932	308	913	377	315	120	187	87	318	123	499	1
II	319	260	309	237	544	331	823	562	365	325	282	240	277	197	432	3
III	106	196	120	244	125	243	164	307	181	343	83	144	68	131	122	2
IV	46	147	59	189	63	208	67	217	63	199	36	127	32	99	54	1
V	25	131	19	100	29	138	30	153	24	120	23	111	17	91	24	1
VI	23	161	16	114	15	102	17	118	16	117	13	91	13	94	15	1
VII	10	79	10	71	8	70	8	68	8	75	6	52	7	56	8	
VIII ...																
Totals ..	818	1,091	853	1,081	1,725	1,402	2,029	1,803	975	1,299	631	852	735	792	1,158	1,2

de less profitable use of the stock in the North
than it could, by giving the stocks too hard
age. What further information does Table III
ovide, for the years since 1930?

It has already been pointed out (Graham 34 b) how the figures of "No." in Table III can used to show the survival from one year to other of particular year-classes and so judge ether fishing is increasing or decreasing, compared with 1921—1930, where the average survival given directly by the ratio of number in successive ar-classes. The survivals which would be calated from Table III differ somewhat for those eady published for some of the years. This is e to some adjustments which we are now in a sition to make, to correct the figures of 1931, 32 and 1933 for the fact that measuring was only ried out during the quarter months of those ars.

Suppose that it is decided to investigate how the hing of 1933—1936 will affect the yield that uld be steadily available, were the fishing of 1933 1936 steadily sustained. This seems a problem t is worth investigation, to which we will ceed. There is, however, one detail that needs ention first. The survival as II-group in 1934 of roup in 1933 is only 40 per cent., whereas the subsequent years, with mesh regulations in ce, gave higher values, 90 and 148 per cent. seems most useful to work with the average of two later years only, in this age-group.

A new letter may conveniently be used here to present the rate of general mortality, that is, tural mortality and fishing together. We have eady (Russell 1931, Graham 1935) A for ruitment, G for growth and M for natural rtality in the whole stock, with small *a*, *g*, and for the same at any given age, as well as C for rate of capture or fishing. For the sake of ort writing V has been used for natural increase, (A + G — M), and it is proposed to have Z d *z* for rate of "decrease", that is (C + M).

Average values of *z* have been worked out from ble III. That from the II-group to the III-group y be given as an example:—

1934/1933		1935/1934		1936/1935	
Fy	C. logs	Fy	C. logs	Fy	C. logs
181	2·2577	83	1·9191	68	1·8325
823	2·9154	365	2·5623	282	2·4502
	—0·6577		—0·6432		—0·6177

—1·9186/3 = —0·6395

—0·6395/0·4343 = —1·4725 = *z*

r the present purpose, the last step may be itted, and the work carried out in common logs, t is with —0·6395 which may be indicated by *z'*.

Construction of the final stock that the rates 1933—1936 would give rise to, from a number of I-group recruits, namely 288, equal to those of 1921—1930, is as follows:—

log 288 =	2·4594 =	log 288	I-group
z' =	0·0613		
	2·5207 =	log 332	II-group
z' =	—0·6395		
	1·8812 =	log 76	III-group
z' =	—0·5103		
	1·3709 =	log 23	IV-group
z' =	—0·4031		
	0·9678 =	log 9	V-group
z' =	—0·2624		
	0·7054 =	log 5	VI-group
z' =	—0·3407		
	0·3647 =	log 2	VII-group

Mere inspection of the two stocks, side by side, shows what a great change has taken place:—

	0	I	II	III	IV	V	VI	VII
1921—1930	1	288	319	106	46	25	23	10
1933—1936	1	288	332	76	23	9	5	2

If we take half the IV and all the older fish as "Large" and also as mature cod, we see that the place of 81 of these fish, valuable both to the present and future fisheries, is to be taken by only 28 fish, or nearly a third. A big reduction is also to be expected in the stock of medium-sized fish. It should be noted that the calculation has the full benefit of any improvement due to the present mesh regulations.

For the time being, however, we are only interested in the respective contributions to the crop of the growth in these two stocks.

The calculation of NWG for the new stock that the fishing of 1933—1936 will produce is generally similar to that for 1921—1930, differing only in one important detail. In 1921—1930 we were able to take the *nw*'s directly from a column of Table III ("Wt"), but for 1933—1936 Table III does not show the correct, permanent *n*'s, which have been found by prophecy in our text, not by observation. Consequently, *w*'s must be calculated separately to apply to the *n*'s. This has been done by dividing the "Wt's" for 1933—1936 in Table III by the "No.'s". The result is:—

	I	II	III	IV	V	VI
w (grammes)	408	758	1,865	3,242	5,053	7,119

The calculations are now the same as before, using the same *g*'s and multiplying to obtain *nwg*'s and adding *nwg*'s to give a new NWG. This works out at *623 kilogrammes per 288 I-group recruits.*

Fishing of the intensity current in 1933—1936 may therefore be expected to result in a substantial *reduction* in the contribution of growth to the crop

of cod, as compared with 1921—1930, when fishing was already unprofitably intense.

The expected reduction in this contribution to the crop is of the order of 20 per cent.

Reference.

Russell, E. S. 1922. Min Agric. and Fish., Fish. Invest. Ser. II, Vol. V, No. 1, London.

Russell, E. S. 1931. Journ. du Conseil, VI, Copenhagen.

*) Bowman, A. 1932. Cons. Perm. Internat. p. l'Explor. de la Mer, Rapp. et Proc.-Verb., Vol. LXXX—III, Copenhagen.

*) Hjort, J. 1932. Cons. Perm. Internat. p. l'Explor. de la Mer, Rapp. et Proc.-Verb., Vol. LXXX—IX, Copenhagen.

*) Hjort, J., Jahn, G. and Ottestad, P. 1933. Hv rådets Skr., VII, 4, Oslo.

Graham, M. *et al.* 1924. Min. Agric. and Fish., F Invest., Ser. II, Vol. VI, No. 6, London.

Graham, M., Carruthers, J. N. and Goodchil H. H. 1926. Min. Agric. and Fish., Fish. Invest., Ser. Vol. VIII, No. 6, London.

Graham, M. and Lumby, J. R. 1929. Min. Agric. a Fish., Fish. Invest., Ser. II, Vol. XI, No. 2, London.

Graham, M. 1934. Min. Agric and Fish., Fish. Inve Ser. II, Vol. XIII, No. 4, London.

Graham, M. 1934 b. Journ. du Conseil, IX, Copenhag

Graham, M. 1935. Journ. du Conseil, X, Copenhagen.

*) Relevant, but not referred to directly in foregoi text.

Addenda.

(1) Figures for 1937, corresponding to those of Table I, became available while this paper was in pres I am glad to say that they show substantial improvement in survival of cod, but sorry that this shoul have been brought about by economic distress in the industry.

(2) *Final Figures of more important Results.*

p. 62

	Year					
	1½	2½	3½	4½	5½	6½
g	1·89	1·04	0·57	0·44	0·39	0·28

p. 64 Table II has been finally corrected.
NWG amounts to 763 kilogrammes per 285 recruits of the I-group.

p. 65

	I	II	III	IV	V	VI	
w	407	762	1,915	3,269	5,010	7,048	grammes

NWG amounts to 620 kilogrammes per 285 recruits.

11

A STUDY OF THE RATE OF GROWTH OF SOME FISHES IN THE BALTIC.

BY

K. A. ANDERSSON.

MAP OF
THE BALTIC
DEPTHS IN METERS.
40 Meters.
80 „ .
200 „ .
400 „ .
12°
14°
16°
18°
20°
22°
24°
65°
64°
63°
62°
55°
Kartsbors
Haparanda
Torneå
Kemi
Luleå
Piteå
Brändöskär
Karlö
Uleåborg
Skellefteå
BOTTEN
BAY
Brahestad
Björöklubb
Umeå
G. Karleby
Nya
Ny Karleby
Kvarken
Örnsköldsvik
Trysunda
Ångerman älven
Norrfällsviken
Nikolaistad
Vasa
Härnösand
Sundsvall
Härnösand
Kaskö
Kristinestad
BOTTEN
SEA
Hudiksvall
Hudiksvall
Kråkön
Söderhamn
Björneborg

Oslo
Raumo
Nystad
Utvalnäs
Gävle
Gryndkallen
Åland
Nådendal
Åbo
Öregrund
Understen
Östhammar
Helsingfors
Ekenäs
Hangö
Uppsala
Norrtälje
Västerås
Yaxholm
Sandhamn
Reval
Baltischport
Karlstad
Kristinehamn
Örebro
Stockholm
Södertälje
Fredriksstad
Fredrikshald
Åmål
Baggensfjärden
Hapsal
Dagö
Koster
Strömstad
Nyköping
Landsort
Nynäshamn
Norrköping
Slätbaken
Emtö
Gotska Sandön
Ösel
Pernau
Hällö
Lysekil
Uddevalla
Vänersborg
Trollhättan
Söderköping
Hjo
Valdemarsviken
Flatvarp
Kappelshamn
Gudingen
Sladö
Visby
Marstrand
Skagen
Göteborg
Jönköping
Västervik
Gamlebyviken
Vinga
Oskarshamn
Gotland
Windau
Kungsbacka
Klintehamn
Östergarn
Läsö
Nidingen
Varberg
KATTEGATT
Falkenberg
Stora Rör
Öland
Riga
Anholt
Halmstad
Kalmar
Laholm
Libau
Kullen
Ängelholm
Karlshamn
Karlskrona
Sölvesborg
Hälsingborg
Helsingör
Landskrona
Copenhagen
Hanö bukten
Memel
Malmö
Trälleb.
Ystad
Själland
Southern Baltic
Middle Baltic
Bornholm
61°
60°
59°
58°
57°
56°
12°
14°
16°
18°
20°
22°
24°

It is very often said that the rate of growth of animals is low when they live in comparatively limited areas of the sea. The Baltic provides us with a good example in this respect. The more one advances into the inner parts of this sea, the smaller the animals are, so it is said. This opinion is in general, sufficiently accurate. But by studying this problem more closely one can also show that the contrary is the case. When external conditions are favourable, the rate of growth may increase as one proceeds from the middle to the inner parts of the Baltic.

I may exemplify this in two cases, the herring and the cod. As regards these fish, I shall compare the rates of growth of samples collected from the area off Nynäshamn in the northern part of the middle Baltic and from the Botten Sea (see the map). As far as we know, migrations of neither of these fishes take place from any of these areas to the other.

Herring.

In his work "The Herring along the Baltic Coast of Sweden"[1]), Hessle, discussing the rate of growth of the herring, points out that owing to great individual variations in the rate of growth, it is difficult to form an accurate judgment on this matter without very plentiful data.

I do not intend to enter into a detailed discussion of the character of the rate of growth of the different races or of the individual changes from year to year. The present study is to be regarded as of a more or less preliminary nature. But I think I have a sufficient amount of material to be able to draw definite conclusions.

I have compared the lengths of equally old specimens of herring (spring spawners and autumn spawners), caught at the same time, some off Nynäshamn in the northern part of the middle Baltic, and some off Hudiksvall and Kråkön in the Botten Sea (see map). Unfortunately fishing in those places is carried on exclusively by nets, and these have, to a certain extent, a selective effect upon the composition of the catches. But as the comparisons in various cases and for different years give similar results, it seems as though no weighty objection can be raised against these results.

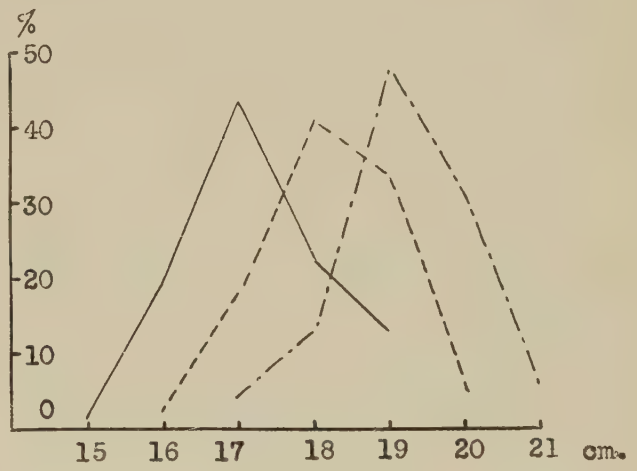


Fig. 1. Length of spring-spawning herring, 5 years old, from the middle Baltic and the Botten Sea.
Middle Baltic ——— Nynäshamn 9. IV 1935
— — — — Nynäshamn 14. V 1935
Botten Sea —·—·—·— Hudiksvall 8. V 1935.

In Fig. 1 the curves show the lengths of five-year-old spring-spawning herrings, taken from two samples from the middle Baltic (Nynäshamn) and from one sample from the Botten Sea (Hudiksvall). They show that the herring is considerably larger in the Botten Sea than in the middle Baltic. The herring of the former area has, at the age of five, an average length of 19·7 cm., and the two samples from the latter area give lengths of 17·26 and 18·20 cm.

In Fig. 2 we find the corresponding length-curves of eight-year-old autumn-spawning herring from the same areas. Here, too, we notice a con-

[1]) Publ. de Circ., No. 89, Copenhague, 1925.

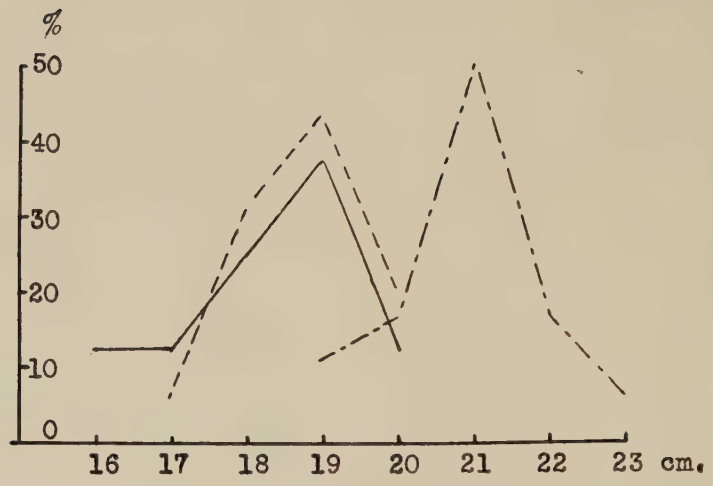


Fig. 2. Length of autumn-spawning herring, 8 years old, from the middle Baltic and the Botten Sea.
Middle Baltic { ———— Nynäshamn 10. IX 1937.
— — — — Nynäshamn 22. IX 1937.
Botten Sea —·—·—·— Hudiksvall 6. XI 1937.

siderable difference between the lengths of the herring from the two areas. The autumn spawning herring has also a higher rate of growth in the northern area, the Botten Sea. The average length was 20·88 cm. in the last-mentioned area and, in the middle Baltic, 18·25 and 18·75 from the two samples.

This difference of size between the two areas is well known to herring fishermen.

Cod.

When, in the early 'twenties, we began to study more closely the Baltic cod, we were surprised to find the largest kind of cod in the northern part of the Baltic — the Botten Sea — in deep water, off Örnsköldsvik. This cod is so big that it reminds one most of the Norwegian "Skrei" in the Lofoten. Hessle has described the rate of growth of the cod in different parts of the Baltic[2]), and Schmidt has given the characteristics of the different cod populations in the Baltic[3]).

On the basis of Hessle's measurements, I have shown in Fig. 3 the curves of the growth-rate of cod from Landsort in the middle Baltic (N. Lat. 58°50′ — E. Long. 18°27′) and from the Ulv Islands in the Botten Sea, off Örnsköldsvik (N. Lat. 63°8′ — E. Long. 18°42′). All these cod were caught in relatively deep water at Landsort in 100—350 m., and off the Ulv Islands in 60—177 m. The growth-curves show clearly that the rate of

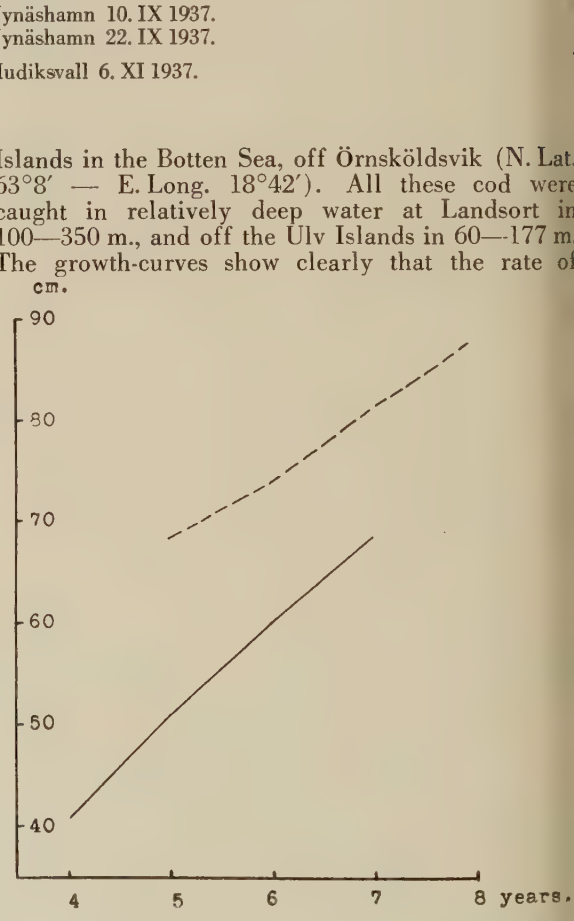


Fig. 3. Rate of growth of cod from the middle Baltic (Landsort) and the Botten Sea (Ulv Islands).
———— Landsort
— — — — Ulv Islands

[2]) Chr. Hessle: Undersökningar rörande torsken (*Gadus callarias*, L) i mellersta Østersjön och Bottenhavet. (With an English Summary). Meddel. Kungl. Lantbruksstyrelsen No. 243. Stockholm, 1923.

[3]) Johs. Schmidt: Raceundersøgelser. X. Den Atlantiske Torsk (*Gadus Callarias* L.) og dens lokale Racer. Meddelelser fra Carlsberg Laboratoriet, Bd. XVIII, No. 6. København, 1930.

owth increases the farther we go into the Baltic.

Now the question is, what factor or, rather, ctors have caused this more rapid growth in the rring and cod of the Botten Sea?

In a paper published in 1923, I gave a general count of the hydrographic conditions in the iddle Baltic and in the Botten Sea[4]). The hydro-aphic conditions of the former area differ totally om those prevailing in the latter.

In the middle Baltic there are two clearly stinct layers of water, an upper one that goes wn to a depth of about 70 m. and a layer lying neath, the greatest thickness of which is about 0 m. In the upper layer, which has a salinity of out 6·5—8·5 ‰, the temperature varies with the asons. The inferior layer, with a salinity of about —10·5 ‰, has a temperature of 4—4·7°, nearly nstant. Perhaps the most remarkable characteri-ic of this inferior layer of water is its very great d constant deficiency of oxygen. The oxygen ntent runs up to only 0·8—1·6 c.c. per litre of ater.

In the Botten Sea, with depths of about 200 m., ere is only one layer of water which can, roughly peaking, be said to correspond to the upper layer the middle Baltic, though with a somewhat lower linity. Shallow banks hinder the lower layer of ater from flowing from the middle Baltic into the otten Sea. The salinity in this area is only ·5—6·4 ‰ and the temperature varies with the asons from the surface to the bottom. The ficiency of oxygen is not noticeable in that area, r if so only to an insignificant extent.

The fact that the main mass of water of the iddle Baltic is stagnant and consequently exhibits all times a great lack of oxygen should render a priori" conditions unfavourable to animal life. should have an especially great effect upon the d which, in the areas of the sea we are dealing ith here, has its actual habitat in deep water, here it also spawns. The cod as a matter of fact an endure the oxygen-poor-water of the middle altic, but all the surroundings of this water may e regarded as unfavourable. Even where all the nimal production is concerned, the hydrographic nditions in the middle Baltic may be regarded s less favourable than in the Botten Sea.

Hessle and Vallin[5]) have also indicated at the production of animal plankton is much reater in the Botten Sea than in the middle Baltic. his might in the first place be due to the fact at this Botten Sea plankton is mostly composed of the two forms *Limnocalanus grimaldi* and *Mysis relicta*, which require a low salinity and a low temperature. The direct result of this great production of animal plankton in the Botten Sea is that the herring gets an abundant supply of excellent food. Hessle and Vallin have also shown that the total catches of herring in the Botten Sea are considerably larger than in the middle Baltic, along equally long stretches of coast.

Where the cod is concerned, the hydrographic conditions play a very important part in the following respect: herring are very seldom found in the stomach of deep water cod from the middle Baltic. This is very likely due to the fact that the herring avoids the inferior layer of water, poor in oxygen. In the Botten Sea, on the other hand, herring is often found in the stomachs of cod from deep water. As there is no bottom water short of oxygen there, it seems as though the herring goes down to great depths.

So, as regards the supply of food, both herring and cod enjoy better conditions in the Botten Sea than in the middle Baltic. Although the low salinity of the Botten Sea should almost be regarded as unfavourable for the herring and for the cod, the abundant supply of food is so predominant a factor that these fishes thrive and grow well.

Plaice *(Pleuronectes platessa)*, Common Dab *(Pl. limanda)*, and Flounder *(Pl. flesus)*.

If the supply of food is of great significance as regards the growth-rate of the herring and cod, the plaice, common dab, and flounder furnish the best example of the dependence of the rate of growth upon the supply of food.

Before the more efficient way of fishing (with the trawl) started in the Bornholm area (southern Baltic) in the early 'twenties, there was a definite overcrowding among these species. The stock consisted of innumerable small fish. But as the stock thinned out, the growth-rate began to rise. The stocks have thus become much better and more valuable.

Molander has given a more detailed account of these facts in relation to the common dab and the flounder and Poulsen as to the growth of the Baltic plaice, and I refer to their investigations joined this paper.

Conclusion.

The food supply seems therefore to exert an influence in two respects:

1) Within the same area the rate of growth decreases in proportion as the stock tends to become overcrowded and the supply of food therefore

[4]) K. A. Andersson: Fiskeribiologiska undersökningar i Östersjön och Bottniska Viken, inledning och allmän översikt. Meddel. Kungl. Lantbruksstyrelsen Nr. 243. Stockholm, 1923.

[5]) Chr. Hessle and Sten Vallin: Undersökningar över plankton och dess växlingar i Östersjön under åren 1925—1927. (With an English summary). Svenska Hydrogr.-Biol. Komm. Skr., N.S.: Biologi, Bd. I, Nr. 5. Stockholm, 1934.

becomes insufficient. To the same extent as the stock thins out, the growth-rate increases. The alteration in the rate of growth would not, however, go beyond the bounds which are characteristic of a species or a variety.

2) In two adjacent areas, the middle Baltic and the Botten Sea, in which the production of food suitable for fish is both quantitatively and qualitatively very different, the herring and the cod have, as has been shown above, a higher rate of grow in the area with abundant supplies of food.

It might also be questioned if the abunda supply of food and the favourable *milieu*, facto which have brought about this abundance, ha not also given rise to the populations of qui growing individuals of herring and cod, which a found in the Botten Sea and possess the anatom characters indicated by Hessle and Schmid

12

ÜBER DAS WACHSTUM DER NUTZFISCHE IM GEBIET DER SÜDLICHEN NORDSEE.

VON

A. BÜCKMANN,
HELGOLAND.

A. Einleitung.

DIE Bedeutung der Kenntnis der Wachstumsgeschwindigkeit der Nutzfische für die grundsätzlichen Fragen der Fischereiforschung beruht darauf, dass das Wachstum (neben der Nachwuchserzeugung) derjenige Faktor ist, der die Substanzvermehrung des Nutzfischbestandes bestimmt. Diese Substanzvermehrung des lebenden Bestandes aber ist es, die unsere Seefischerei ausnutzt und für die menschliche Ernährung verfügbar macht. Wollen wir wissen, bei welcher Art und Stärke der Befischung die Substanzvermehrung des Bestandes und damit der Ertrag der Fischerei am grössten ist, so müssen wir offenbar das Wachstum kennen.

Die Überlegungen, die die Frage nach dem höchstmöglichen Ertrag der Fischerei und seiner Beziehung zum Wachstum erfordert, sind zu verwickelt und zu umfangreich, als dass sie hier dargelegt werden könnten. Der Verfasser hat deshalb an anderer Stelle einen Versuch veröffentlicht, die grundsätzliche Seite dieses Problems zu erörtern. Er gelangt dazu, in der von M. Graham vorgeschlagenen Methode einen praktisch bedeutsamen Fortschritt zu sehen. Diese Methode — wie jede, die das Problem nicht experimentell angreift — geht von einer Anzahl von Voraussetzungen und approximativen Annahmen aus; es scheint nun unter unseren Aufgaben die dringlichste zu sein, zu prüfen, ob bei den einzelnen von uns untersuchten Nutzfischbeständen diese Annahmen zulässig sind. Wenn ja, so sollte die Methode Grahams angewendet werden, um zu prüfen, ob die gegenwärtige Befischung der Bestände schon den Punkt überschritten hat, bei dem auf die Dauer der höchstmögliche Ertrag erzielt wird.

Wir verdanken M. Graham einen Beitrag, in dem die Anwendung seiner Methode auf den Kabeljaubestand der Nordsee in einleuchtender Weise vorgeführt wird. Die Arbeit Grahams ist auf S. 57 abgedruckt, sodass weitere Erörterungen darüber nicht vonnöten sind. Es mag der Hinweis genügen, dass man die praktische Bedeutung der Wachstumsbestimmungen garnicht besser beweisen kann als durch die von Graham vorgelegten Berechnungen.

Der vorliegende Bericht bezweckt nur eine Zusammenstellung der tatsächlichen Beobachtungen über die Wachstumsverhältnisse der Nutzfische in unserm Gebiet. Der Verfasser hat sich der Unterstützung der an den Untersuchungen beteiligten Sachverständigen erfreuen dürfen, die ihm Materia und Ausarbeitungen in verschiedenem Umfang zu Verfügung gestellt haben. Folgende Beiträ gingen ein:

Erdmann, W. Hering.
Graham, M., Kabeljau (Dieser Band, Beitra No 10, S. 57).
Hickling, C. F., Scholle (Markierungsexper mente).
Hodgson, W. C., Hering (Vergl. S. 76).
Jensen, Aage J. C., Scholle und Scharb (Dieser Band, Beiträge Nos. 15 u. 16).
Tesch, J. J., Hering, Scholle, Scharbe.
Thursby-Pelham, D. E., Scholle.
Schmidt, U., Scholle und Seezunge.

Ausser diesen Beiträgen wurden besonders di folgenden Veröffentlichungen benutzt:

Bückmann, A., Untersuchungen über die Natur geschichte der Seezunge. Ber. Deutsch. wiss Komm. f. Meeresf., N.F., 7/2, 1935.
Bückmann, A., und Kotthaus, A., Ein Vergleich der Schollenbevölkerung der Flä mischen und der Deutschen Bucht. Rapp. e Proc.-Verb., Vol. XCIV, 1935.
Le Gall, J., Le Hareng. Ann. Inst. Occanogr Paris T. XV, F. 1, 1935.
Le Gall, J., Statistiques biologiques et Considé rations sur les Populations de Harengs etc. Rev Trav. Off. Pêches Marit., VIII, 1, (1935); IX 1, (1936); X,1, (1937).
Gilson, G., Recherches sur la Biologie du Hareng guai etc. Inst. Etudes mar. d'Ostende, Mem. 1 Lier, 1931.
Graham, M., Report on North Sea Cod. Min. Agric. Fish., Fish. Invest., (II) XIII, 4, 1934.
Hodgson, W. C., Investigations into the Age Length, and Maturity of the Herring etc. III. Min. Agric. Fish., Fish. Invest., (II), XI, 7, 1929.
Jensen, Aage J. C., The Effect of the Plaice Fishery etc. Rapp. et Proc.-Verb., Vol. LXXX 1932.
Poulsen, E. M., Biology of the Dab in Danish Waters. Rep. Dan. Biol. Stat., XXXVIII, 1933.
Robertson, I. A., A preliminary Account of the Sprat and Sprat Fishery in England. Journ. du Conseil, IX, 1936.
Thursby-Pelham, D. E., Report on English Plaice Investigations etc. Min. Agric. Fish. Fish. Invest., (II), XII, 5, 1932.

B. Methodische Vorbemerkung.

Das Wachstum der Fische kann auf zweierlei ise bestimmt werden: Einmal durch Berechnung Durchschnittslänge oder Bestimmung der Lage Gipfels der Längenvariation der Fische jeder zelnen Altersgruppe zu bestimmten Jahreszeiten. n anderen durch Berechnung des Längenzu- hses markierter Fische während der Zeit ihres ilebens. Material der letztgenannten Art liegt genügendem Umfang aus unserem Gebiet nur die Scholle vor.

Beide Methoden haben ihre Fehlerquellen. se liegen vor allem in der selektiven Fang- kung der Netze, die zur Probenbeschaffung utzt werden, und in der Ungleichmässigkeit der benentnahme. Bei der Beurteilung der weiter en mitgeteilen Befunde sollten folgende Punkte ücksichtigt werden:

1. Es gibt kein Gerät, das eine Probe des standes in genau der gleichen Zusammensetzung gt, wie sie im Meere am Fangort vorhanden ist. r wissenschaftliche Fänge werden bisweilen räte verwendet, die darauf berechnet sind, eine glichst repräsentative Fangprobe zu liefern. glicherweise ist hier der Fehler der Probe hältnismässig klein. Die Geräte der praktischen cherei sind darauf berechnet, untermassige Fische kommen zu lassen. Schon der unsortierte Fang hält hier im allgemeinen im Verhältnis zu wenig ine Fische. Infolgedessen wird die Durch- nittslänge jeder Altersgruppe, die noch unter- ssige Fische enthält, zu hoch veranschlagt rden. Die Durchschnittslänge der Altersgruppen einer vom Fischer sortierten Marktanlandung d noch grössere Abweichungen zeigen.

2. Da die untermassigen Fische, soweit sie angen werden, über Bord geworfen werden und ht dem Fischer einzeln durch die Hand gehen, ist das Auffinden eines wiedergefangenen mar- rten, noch untermassigen Fisches Zufallssache. weit die Fische nicht schon in marktfähiger sse ausgesetzt wurden, müssen die eingelieferten ederfänge daher vorzugsweise Plusvarianten des chstums sein und somit einen zu grossen Durch- nittswert des Zuwachses pro Jahr liefern.

3. In manchen Fällen wachsen die Fische nicht ganzen Meeresgebiet gleich schnell, sondern es d Gebiete schnellen und langsamen Wachstums unterscheiden. Es hat dann keinen Zweck, die rchschnittliche Wachstumsgeschwindigkeit für ganzen Bestand zu bestimmen. Ein Wachstum, den berechneten Mittelwerten entspräche, kommt ir Wirklichkeit garnicht vor.

4. Methodisch schwieriger sind die Fälle, wo Plus- und Minusvarianten des Wachstums sich hr oder weniger voneinander sondern. Bei der olle z. B. wandern die schneller gewachsenen ividuen eher von den flachen Sandgründen der ste nach den mittleren, tieferen Teilen unseres biets ab als die langsam gewachsenen. Die Durchschnittslänge der Altersgruppen in jedem Teilgebiet gibt daher nicht ein richtiges Bild von den wirklichen Wachstumsverhältnissen. Eine Kombination der Teilbeobachtungen im richtigen Verhältnis ist u. U. sehr schwierig. — Ähnlich ist es, wenn sich die besser- und die schlechtergewachsenen Individuen gleichen Alters verschiedenen Schwärmen anschliessen, wie das beim Hering vorkommt. Die zum Laichen sich scharenden Fische aller Arten werden von den Altersgruppen, die zum Teil noch nicht geschlechtsreif sind, vorzugsweise schnellwüchsige Individuen enthalten.

5. Die praktische Fischerei stellt vorzugsweise den grösseren Fischen nach. Ihre Fänge werden von den jüngeren Altersgruppen hauptsächlich die Plusvarianten des Wachstums enthalten. Erst in höherem Alter werden die Minusvarianten in vollem Umfange in Erscheinung treten. Nun werden aber die Plusvarianten einen zu geringen Anteil stellen, weil die Mehrzahl von diesen schon früher weggefangen ist.

6. Wie der von der Ergiebigkeit des Fanges diktierte Wechsel der Fangplätze der praktischen Fischerei auf die Durchschnittslängen der Altersgruppen in den Anlandungen wirkt, davon vermittelt uns Fig. 7—10 einen deutlichen Eindruck. Wir sehen hier die Durchschnittslänge der Schollen jeder Altersgruppe in englischen Marktanlandungen in den Monaten Juni, September, Dezember, März dargestellt (Nach Thursby-Pelham, MS.). Die Längen nehmen keineswegs in einer dem jahreszeitlichen Wachstum entsprechenden Kurve zu, sondern es entsteht eine Zickzacklinie. Insbesondere sind die Durchschnittslängen der Altersgruppen im Winter (Dezember, bisweilen auch März) meist höher als im nachfolgenden Frühling. Es wird im Winter mehr auf den tieferen Gründen und auf geschlechtsreife Fische gefischt, im Frühling mehr auf den flachen Gründen, wo sich die unreifen Schollen dann sammeln.

7. Die tatsächliche Wachstumsgeschwindigkeit der Fische ist vielfach nicht so gross, wie ihre erbliche Konstitution es erlauben würde ("Potentielles Wachstum" Strodtmanns). Vielmehr wird die realisierte Wachstumsgeschwindigkeit durch äussere Bedingungen bestimmt. Von solchen Bedingungen sind in konkreten Fällen als wirksam nachgewiesen die Temperatur der Umgebung, die ja ganz allgemein die Geschwindigkeit des Ablaufs der Stoffwechselvorgänge bestimmt, und die Menge der vorhandenen Nahrung, die dem einzelnen Fisch im Durchschnitt zur Verfügung steht. Beide Faktoren können veränderlich sein und damit Veränderungen in der realisierten Wachstumsgeschwindigkeit herbeiführen.

8. Die Menge der auf den einzelnen Fisch entfallenden Nahrung kann nachweislich mit den Fluktuationen im Bestande der Nährtiere schwanken. Es kommen aber für jede Fischart verschiedene Nährtierarten infrage, und die Fluktuationen der

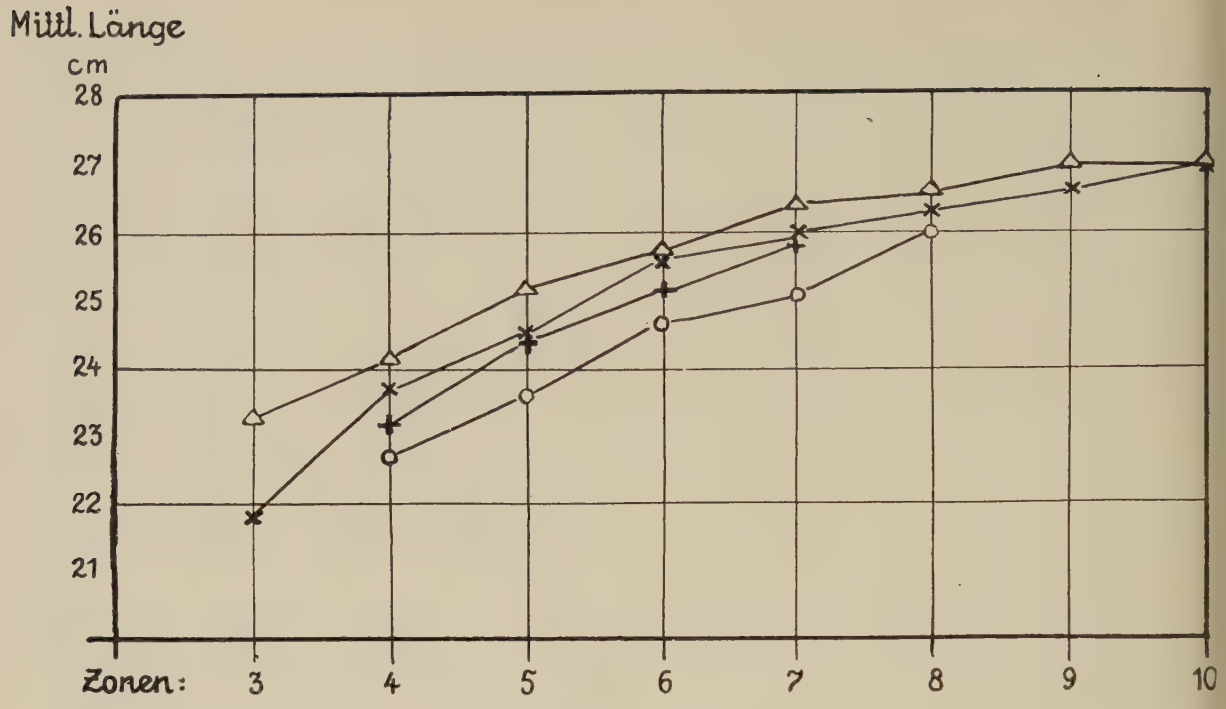


Fig. 1. Durchschnittslängen von Heringen verschiedenen Alters im ostanglischen Fanggebiet (nach Hodgson).

× Durchschnittslängen in den Proben von 1934.
△ Durchschnittslängen in den Proben von 1937.
○ Durchschnittslängen des Jahrgangs 1921.
+ Durchschnittslängen des Jahrgangs 1922.

Nährtiere brauchen nicht im ganzen Gebiet gleichsinnig zu verlaufen. Das dürften die Gründe sein, weshalb Wachstumsänderungen von Nutzfischen im Zusammenhang mit den Fluktuationen ihrer Nährtiere bisher nur für kleine Gebiete nachgewiesen worden sind.

9. Die Menge der auf den einzelnen Fisch entfallenden Nahrung kann sich aber auch im Zusammenhang mit der Zahl der vorhandenen Fische der betreffenden Art verändern. Wachstumsschwankungen, die hierauf zurückzuführen sind, sind bei den Schollen auf den Jungfischgründen der südöstlichen Nordsee nachgewiesen worden. Diese Gebiete sind verhältnismässig arm an Nährtieren, während die Besiedlung mit Schollen bisweilen sehr dicht werden kann. Da ferner während der Wachstumsperiode der Schollen die Temperatur des Bodenwassers im Vergleich mit anderen Gebieten sehr hoch ist, leuchtet es ein, dass in diesem Falle die Nahrung der Minimumfaktor ist, der das Wachstum bestimmt, und dass die vorhandene Nahrungsmenge einem sehr dichten Bestande nicht die gleiche Wachstumsgeschwindigkeit ermöglicht wie einem dünneren. Bei den anderen Nutzfischen der südlichen Nordsee, wie auch bei den Schollen in anderen Teilgebieten, ist eine Beziehung zwischen der Bevölkerungsdichte der Fische und ihrer Wachstumsgeschwindigkeit nicht festgestellt worden.

C. Die Wachstumsverhältnisse der einzelnen Fischarten.

I. Hering. *(Clupea harengus).*

1. Bezüglich der Wachstumsverhältnisse der Heringe des ostanglischen Gebiets folgen wir der Darstellung von W. C. Hodgson (MS.):

The study of the growth-rate of the herrings from this area presents a very difficult problem indeed, for, while it has been found that the general trend of the growth-curves for several year-classes is fairly constant, the actual lengths of the fish of different year-classes vary considerably at each age.

We find that the herrings grow rapidly up to the age of about four years and after that there is a diminution in the annual increment, and this agrees with the main age at which the fish become mature.

In the diagram are drawn length-curves for the fish of various ages from three upwards in the catches of 1934 and 1937, together with the growth curves for herrings of the 1921 and 1922 year classes (Fig. 1). It will be seen that there is considerable difference between the lengths of the fish at the same apparent age. For instance the length of the 1921 year-class herrings at any age, *n*, is approximately equal to the length of the 1922 year-class herrings at the age of *n*—*1*. Such variations may at first be considered to be due to differences in the rate of growth, but I believe that, since the trend of the curves is constant, the growth-rate is similar in all cases, and the difference at each age depends entirely on the time of

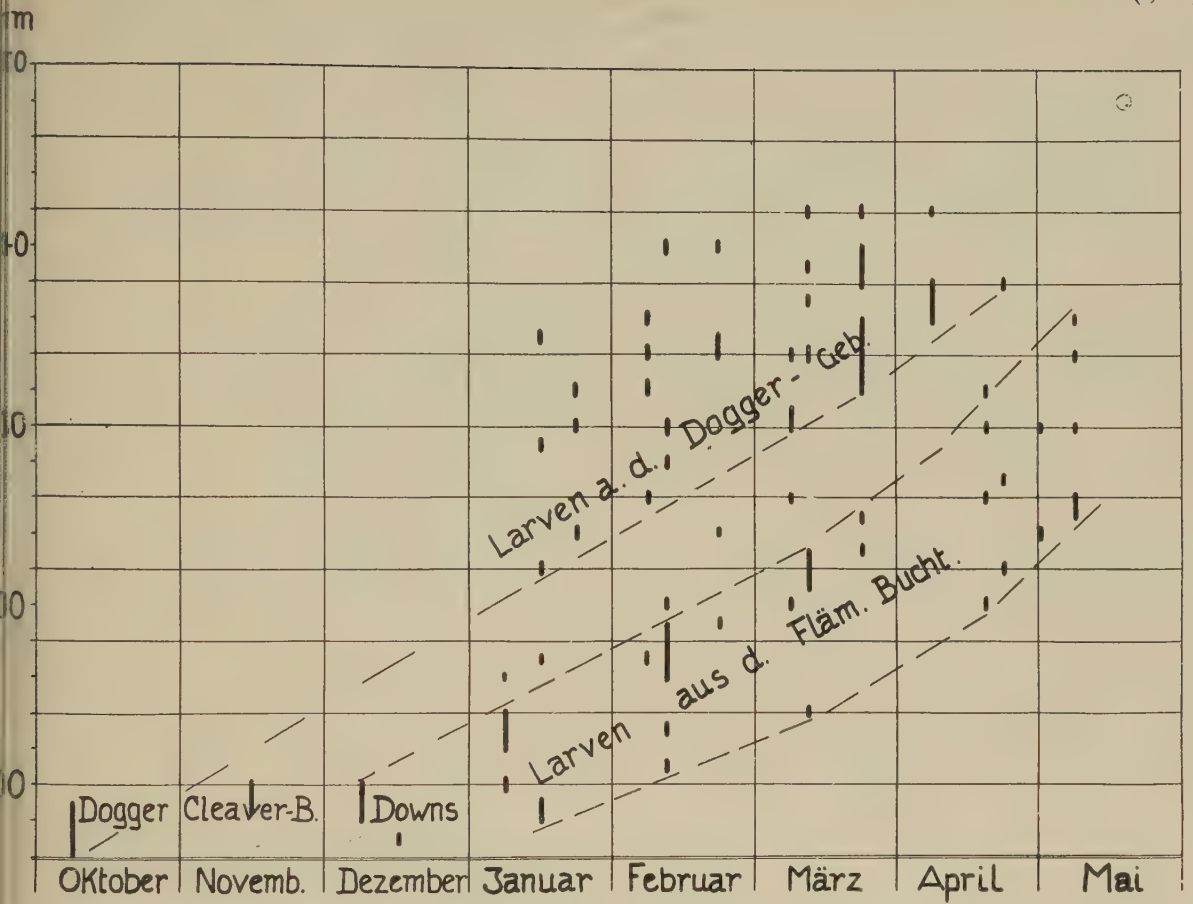


Fig. 2. Lage der Gipfel der Längenvariation der Heringslarven in der südlichen Nordsee nach den deutschen Untersuchungen. Schematisch.

ar in which the year-class was born. In other ords the differences may be related to the ngth l_1.

I have shown (l.c. pp. 50—52) that the 1921 ar-class had a length l_1 of 7—8 cm., while that the 1922 year-class was 9—10 cm. This, I lieve, shows that the former were winter-born fish om the eastern end of the Channel, and the latter ere autumn-born fish from further north, probably e Dogger region. Thus, in the growth-curve, the 921 year-class fish and the 1922 year-class fish the ages shown were not actually the same age. he 1921 fish are, at the point "4", about four ea s old, but the 1922 fish are about four years d three or four months old. It will be clear om this that it is not correct to give a growth- rve for Southern North Sea herrings without king into consideration the time at which the fish ere born.

The length of herrings with three zones on their ales is very difficult to assess, because the length epends on the strength of the year-class compared ith the number of four-year-old herrings present in the shoals. If there are only a few of the three-year-old herrings compared with the four's then the length will be much greater than if there are many three's.

To summarize, the length of the herrings at any given age, as determined by the number of growth-zones on the scales, depends on

(1) the time at which the fish were born.
(2) The numerical strength of the year-class in comparison with other year-classes in the shoals.
(3) The size of mesh of the drift-nets which caught them.

From the above it is apparent that there are several types of herrings in the East Anglian shoals, if length for age is taken as a criterion.

In der citierten Arbeit hat H o d g s o n ferner mitgeteilt, dass den auf Grund von Schuppenmessungen festgestellten Gipfeln der Variation von l_1 auch Gipfel in der Längenvariation der an der

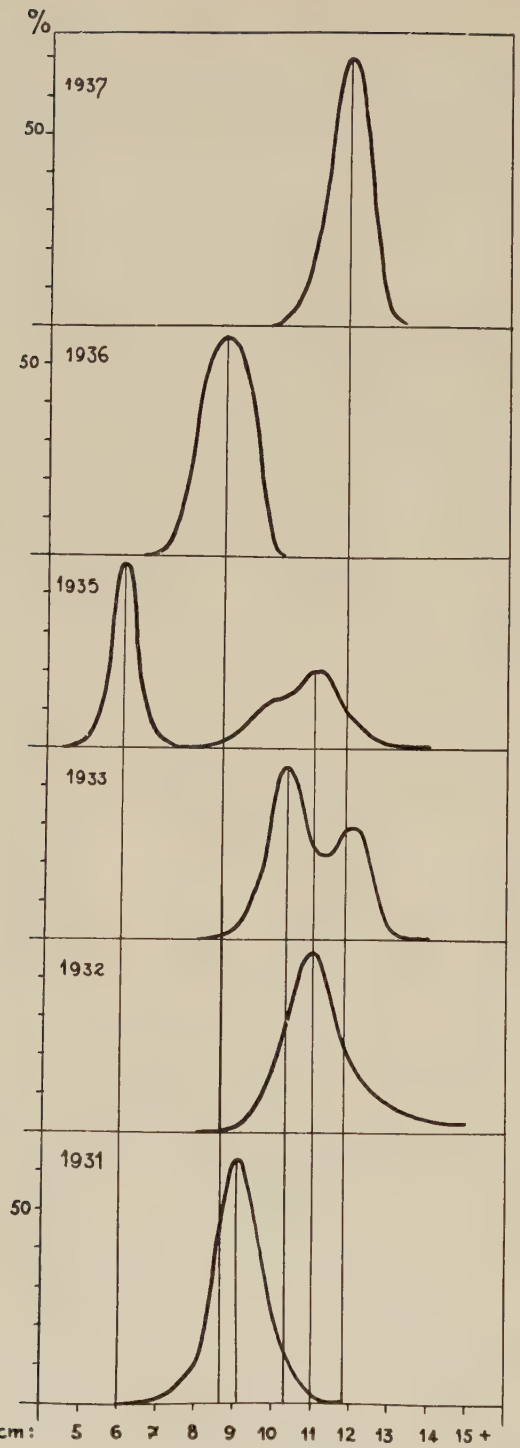


Fig. 3. Längenvariation der Jungheringe in der Deutschen Bucht im Mai verschiedener Jahre.

englischen Küste gefangenen Jungheringe entsprechen. Ausser den erwähnten Hauptgipfeln beobachtet er kleinere Höhepunkte bei den Längen von ca. 5 und ca. 13 cm. Er vermutet, dass diese Fische einem Spätsommerlaichen (Juli/August) an der englischen Ostküste entstammen, die bis zum Herbst z. T. bereits Schuppen gebildet haben, sodass der erste Winter ihres Lebens die erste Winterlinie hervorruft, z. T. aber auch noch unbeschuppt überwintern, sodass die erste Winterlinie erst bei einem Alter von fast 1½ Jahren entsteht.

2. Es ist eine einleuchtende Annahme, dass die später im Jahre geborenen Heringe jeweils kleiner sein sollen als die früher geborenen. Bei den deutschen Untersuchungen hat es sich gezeigt, dass die aus der flämischen Bucht und dem Kanaleingang stammenden Winterlarven bis zum Mai hin bei Berücksichtigung der regionalen Verteilung auf Grund ihrer geringeren Grösse recht gut von den Spätsommer- und Herbstlarven aus der weiteren Umgebung der Doggerbank unterschieden werden können (Vergl. die schematische Fig. 2). Auch beobachten wir in verschiedenen Jahren verschiedene Gipfel der Längenvariation bei den Jungheringen der Deutschen Bucht. Fig. 3 zeigt die im Mai verschiedener Jahre festgestellte Grössenzusammensetzung (also zu Beginn der neuen Wachstumsperiode). Der Gipfel bei 9 cm. (1931 und 1936) kann wohl dem bei Hodgson beobachteten Modus von $l_1 = 7$—8 cm. entsprechen, der bei 11—12 cm. (1933, 1935, 1937) dem Modus von $l_1 = 9$—11 cm. Die 6 cm. langen Heringe des Jahres 1934 waren, soweit festgestellt, noch unbeschuppt und können einem Spätsommerlaichen entstammen, dessen Abkömmlinge nicht jedes Jahr in die Deutsche Bucht gelangen.

3. Erdmann (MS.) teilt die Durchschnittslängen von Heringen mit, die im Herbst im Doggerbankgebiet gefangen worden sind. Zum allergrössten Teil sind es nachweislich Herbstlaicher dieses Gebiets. Die Werte der beiden Jahre 1934 und 1935 unterscheiden sich nicht wesentlich voneinander:

Wirkl. Alter, Jahre:	1934		1935		1934/1935	
	Anzahl	M. L.	Anzahl	M. L.	Anzahl	M. L.
2	43	18·9	15	19·2	58	18·97
3	580	21·7	433	22·1	1013	21·87
4	347	23·9	357	24·0	704	23·95
5	368	24·8	159	25·5	527	25·01
6	241	26·1	252	25·8	493	25·94
7	68	26·3	167	26·5	235	26·44
8	23	26·9	68	27·0	91	26·97

4. J. J. Tesch (MS.) teilt die Durchschnittslängen von Heringen mit, die im Herbst und Winter (Okt.—Febr.) in der südwestlichen Nordsee (südl. von 53°30′) und im Ostteil des Kanals gefangen sind. Auch hier sind die Unterschiede in den Längenmitteln der drei Jahre 1934—1936/37 recht gering.
Die Durchschnittslängen dieser Heringe sind deutlich höher als die der Doggerbankheringe Erdmanns.

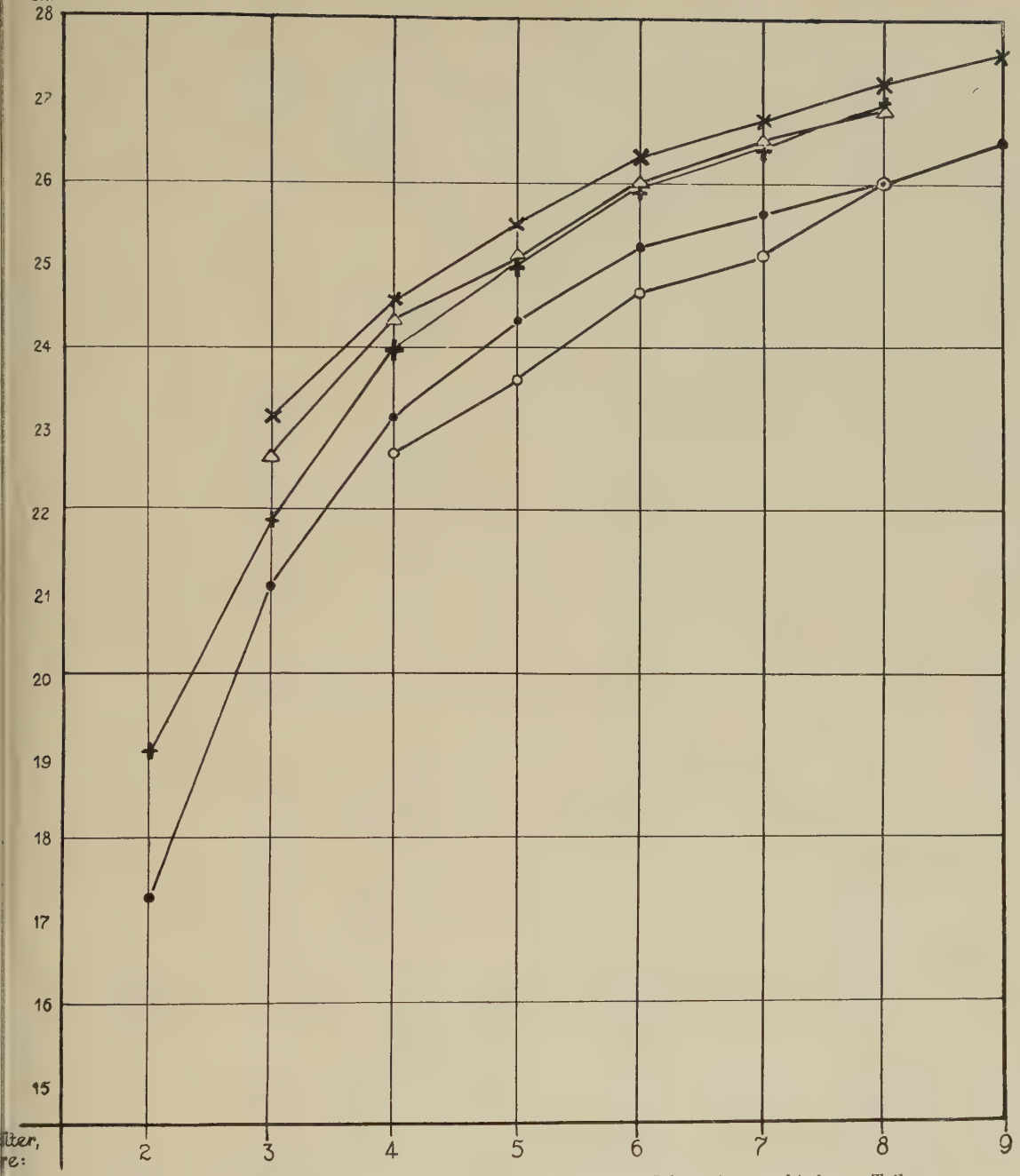


Fig. 4. Durchschnittslängen der Heringe im Alter von 2—9 Jahren in verschiedenen Teilen der südlichen Nordsee.

Doggerbankgebiet 1934—35 nach Erdmann.
Südwestliche Nordsee und Kanaleingang 1934—37 nach Tesch.
Südwestliche Nordsee und Kanaleingang 1934—37 nach Le Gall.
Ausgelaichte Heringe der belgischen Küste 1930—31 nach Gilson.
Jahrgang 1921 im ostanglischen Gebiet nach Hodgson.

Wirkl. Alter Jahre:	1934/35 Anz.	M.L.	1935/36 Anz.	M.L.	1936/37 Anz.	M.L.	1934/37 Anz.	M.L.
3	229	23·1	688	23·6	84	23·2	1001	23·09
4	469	24·41	1114	24·2	1153	25·0	2736	24·56
5	1431	25·4	391	25·5	831	25·5	2653	25·43
6	432	26·3	806	26·3	397	26·4	1635	26·30
7	287	26·8	275	26·9	619	26·7	1181	26·77
8	86	27·3	136	27·3	119	27·2	341	27·25
9	27	27·8	44	27·9	64	27·3	135	27·58

5. Wenn man auch zugibt, dass Heringe, die aus dem Herbstlaichen im Doggerbank—Yorkshiregebiet stammen, an dem Winterlaichen im Downsgebiet teilnehmen können und umgekehrt, so wird man doch erwarten, dass in jedem Gebiet vorzugsweise einheimische Heringe laichen. Sowohl Gilson (l.c.) wie Le Gall (l.c.) finden aber bei der Untersuchung der Schuppen ausgelaichter bzw. laichender Downsheringe, dass der Durchschnittswert von l_1 bei 10 cm. liegt, nicht bei 7—8 cm., wie man nach Hodgsons Anschauung erwarten sollte.

6. Unser Diagramm Fig. 4 gibt (a) die Durchschnittslängen wieder, die von Erdmann für Doggerbankheringe angegeben werden (Mittel 1934/35), ferner (b) Teschs Mittelwerte von Heringen der südwestlichen Nordsee und des Kanaleinganges (Mittel 1934—1937), sowie (c) die Mittelwerte, die sich aus Le Galls Angaben für sein gesamtes Untersuchungsgebiet (Groupe Dyck, Groupe I und Groupe II) im Mittel der Jahre 1934—1936 ergeben. Das ganze Gebiet durfte zusammengefasst werden, weil die Unterschiede zwischen den drei Gebieten, auf die er früher hingewiesen hat, in den berücksichtigten Jahren unerheblich waren. Weiter sind (d) die Durchschnittslängen dargestellt, die von Gilson nach Schuppenmessungen für den ausgelaichten Hering der belgischen Küste angegeben worden sind. Zum Vergleich sind endlich Hodgsons Durchschnittslängen des Jahrgangs 1921 unter den ostanglischen Heringen eingezeichnet.

Von diesen sind Teschs Werte die höchsten. Le Galls, die sich etwa auf dieselben Heringe beziehen, liegen sehr ähnlich, nur einige mm. tiefer. Vielleicht kann man den Unterschied schon mit verschiedener Technik der Probenentnahme und dem persönlichen Fehler erklären. Der Verlauf der Wachstumskurve Gilsons ist wiederum ausserordentlich ähnlich wie die vorgenannten, doch liegen seine Werte deutlich, etwa um einen cm., tiefer als Le Galls. Bemerkenswert ist es, dass einerseits die von Erdmann festgestellten Werte z. T. völlig mit Le Galls zusammenfallen, obwohl es sich um Heringe ganz verschiedener Herkunft handelt. Nur im Alter von 3 und 4 Jahren sind die Doggerbankheringe etwas kleiner als die Downsheringe. Andererseits waren die Heringe des ostanglischen Gebiets — Jahrgang 1921 — in gleichem Alter wesentlich kleiner als die Downsheringe und als die Doggerbankheringe. Dagegen würden die Durchschnittslängen, die Hodgson 1937 bei den ostanglischen Heringen feststellte, sehr gut mit den Winterheringskurven zusammenfallen.

Die Verhältnisse sind also offenbar recht verwickelt und erfordern noch weiteres Studium.

II. Sprott *(Clupea sprattus)*.

Untersuchungen über das Wachstum des Sprotts werden in der südlichen Nordsee bisher nur von englischer Seite systematisch durchgeführt. I Erwartung einer ausführlichen Arbeit von I. A Robertson beziehen wir uns auf die von ih a. a. O. veröffentlichten vorläufigen Angaben, di in der Wachstumskurve Fig. 5 dargestellt sind.

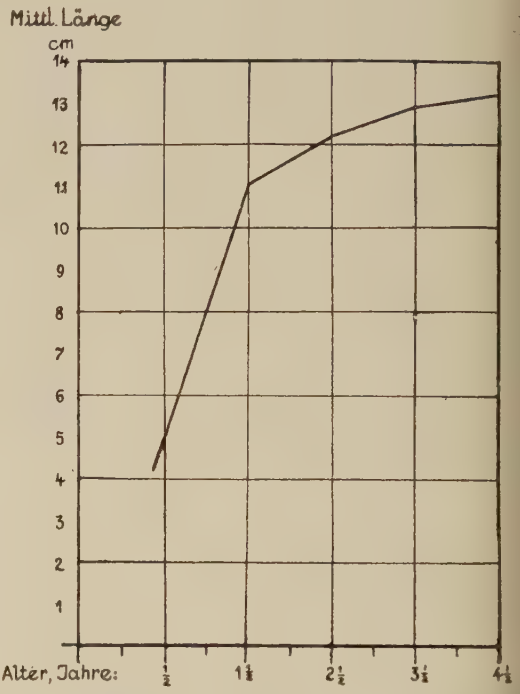


Fig. 5. Wachstum des Sprotts an der Ostküste England (nach Robertson).

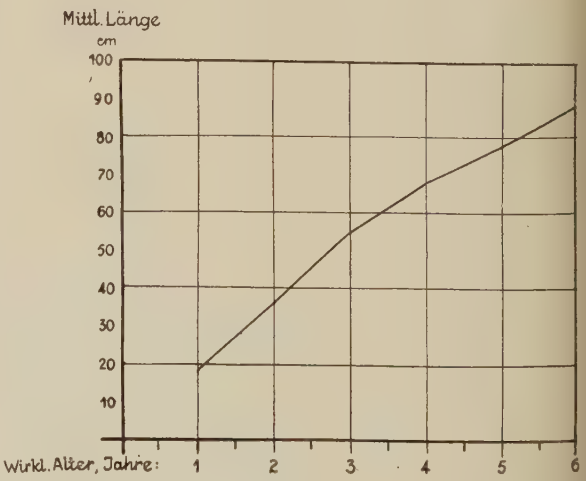


Fig. 6. Wachstum des Kabeljaus in der südlichen Nordsee (nach Graham).

. **Kabeljau *(Gadus morrhua).***

Über die Wachstumsverhältnisse des Kabeljaus in der als No. 10, S. 57, gedruckten Arbeit von r a h a m Näheres zu finden. Zum Vergleich mit n Daten für die anderen Fische ist hier nur die m gleichen Autor in seiner früheren Arbeit gegebenen Serie der Durchschnittslängen auf- führt. Es handelt sich hierbei um den schnell- ichsigen Typ, den wir nach G r a h a m s Befun- n als in der südlichen Nordsee absolut vor- rrschend ansprechen dürfen.

ter in vollen Jahren: 1 2 3 4 5 6
ittl. bezw. häuf. Länge: 18 36 55 68 78 89 cm.

ergl. auch Fig. 6.

. **Scholle *(Pleuronectes platessa).***

1. Bei der Scholle suchen, wie erwähnt, die sser gewachsenen Individuen vorzugsweise tieferes asser auf. Die Durchschnittslängen der Alters- uppen sind in tieferem Wasser jeweils grösser als flacheren. Hierfür 2 Beispiele: —

rchschnittslänge der Schollen ♂+♀ im Gebiet vor der nordfriesischen Küste, Mai 1937.
(Schmidt, M. S.)

assertiefe:	Altersgruppe I	II	III	IV
—15 m.	8·8	14·1	18·3	22·3
—25 m.	9·5	15·2	19·3	22·7
—40 m.	—	16·2	20·7	24·4

Durchschnittslänge der Schollen im Winter und Frühjahr 1936 (Kotthaus MS.)

Wassertiefe:	Jahrgang:	1934	1933	1932	1931	1930	1929
über 40 m.	(Februar)	15·1	18·2	21·5	25·1	26·6	29·0
0—40 m.	(Mai/Juni)	13·2	17·3	21·7	24·6	24·8	26·0
über 40 m.	(Februar)	15·8	19·2	22·4	25·3	28·3	29·5
0—40 m.	(Mai/Juni)	13·2	17·6	22·2	24·8	27·5	27·3

Die Schollen des tieferen Gebiets waren also mit er Ausnahme bereits im Februar grösser als die s flacheren im Mai/Juni, d.h. etwa zwei Monate ch Beginn des neuen Wachstums.

Infolge der Abwanderung der besser gewachse- n Individuen kann in den flacheren Gebieten gar ein Rückgang in der Durchschnittslänge des rgangs eintreten:

Durchschnittslänge der Altergruppen in Area A_2 und B_3 (Tesch, MS. nach Redecke 1909)

rsgruppe:	I			II			III	
eszeit:	H.	W.	S.	H.	W.	S.	H.	W.
ea A_2	15·6	**13·1**	16·0	18·4	**16·2**	21·3	24·0	—
B_3	17·4	**16·6**	17·6	20·3	20·5	21·6	24·8	25·1

Die Zunahme der Durchschnittslängen auf den gschollengründen ist demnach sicher kleiner als s wirkliche durchschnittliche Wachstum.

2. Die Durchschnittslänge gleichalter Schollen ist in verschiedenen Abschnitten der Jungschollen- gründe verschieden:

Durchschnittslängen der Altersgruppen in verschiedenen Abschnitten der Jungschollengründe.
5-jährige Mittel.
(Bückmann u. Kotthaus l. c.)

Altersgruppe:	II	III	IV	V
Vor der nordfr. Küste ..	12·6	15·9	19·6	22·5 cm.
„ „ ostfr. „ ..	13·2	17·0	21·0	24·1 cm.
„ „ westfr. „ ..	16·2	20·5	23·6	26·5 cm.
„ „ Küste von Nord- holland	17·6	20·7	23·9	27·9 cm.

Diese Erscheinung kann auf Unterschiede in der Wachstumsgeschwindigkeit, möglicherweise aber auch auf Unterschiede in der Abwanderung der schnellwüchsigen Schollen zurückzuführen sein falls diese in den südlicheren Gebieten jeweils näher an der Küste bleiben.

Nach H i c k l i n g (MS.) liefern nämlich die englischen Markierungsexperimente der Jahre 1928—33 keinen Anhaltspunkt dafür, dass die Schollen im Gebiet von Hornsriff und der inneren Deutschen Bucht langsamer wüchsen als im Gebiet vor der Küste der Niederlande. Er schreibt: "Generally speeking, fish marked in the Hornsreef—Sylt area grew more rapidly than those marked of Norderney—Terschelling and the Haaks." "As an average of all experiments in the years 1929—32, the increments of growth made by marked plaice were at the end of the first year:—

At the Stations:	Jutland coast	Heligoland,	Frisian coast,	Haaks
cm.:	3·8	3·7	3·4	3·0

3. Es sei kurz darauf verwiesen, dass die weibliche Scholle schneller wächst und grössere Endlängen erreicht als die männliche. Die Bestätigung hierfür ist aus den Diagrammen Fig. 6—8 zu entnehmen. In den ersten Lebensjahren ist der Grössenunterschied noch gering. Es ist daher zulässig, für diese Jahre Gesamtmittel von ♂ + ♀ zu bilden.

4. Innerhalb der Deutschen Bucht ist die Durchschnittslänge der Schollen gleichen Alters erheblichen Schwankungen unterworfen. Es erreichten die einzelnen Jahrgänge im Frühjahr des 3.—6. Lebensjahres folgende Durchschnittslängen (B ü c k m a n n, K o t t h a u s, S c h m i d t, MS.):

Altersgruppe:	II	III	IV	V
Jahrgang 1926:	14	19	24	26
„ 1927:	14	19	22	24
„ 1928:	13	17	19	22
„ 1929:	13	16	19	22
„ 1930:	13	17	20	23
„ 1931:	14	17	21	25
„ 1932:	14	19	22	26
„ 1933:	14	18	23	—

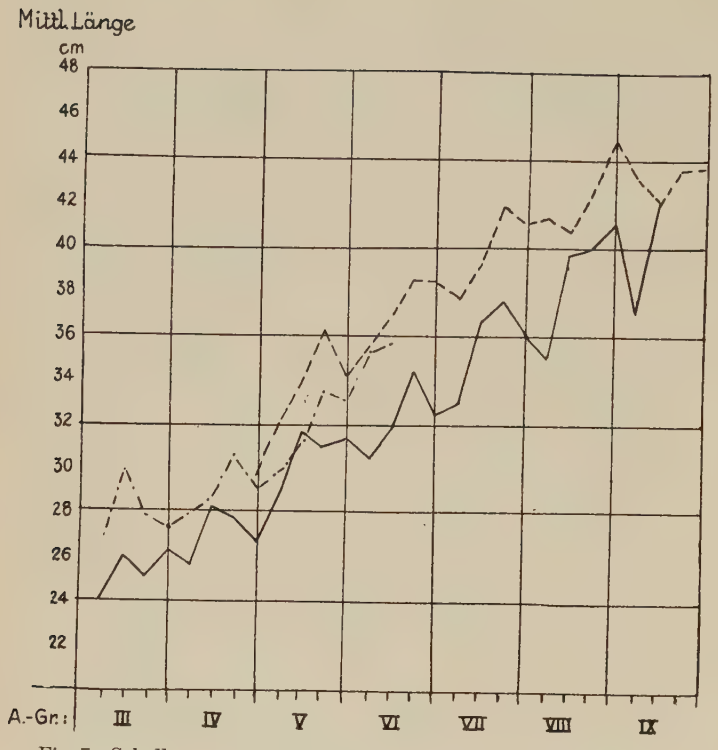


Fig. 7: Schollen ♀, Jahrgang 1926 ---, 1928 ——, 1931 -·-·-.

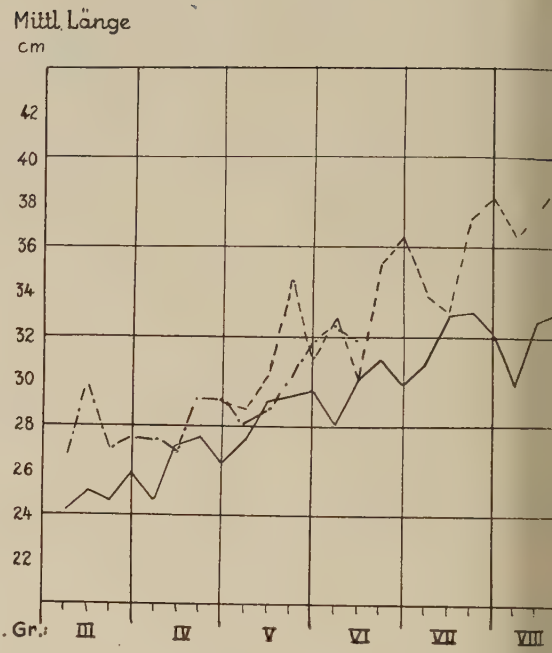


Fig. 8: Schollen ♂, Jahrgang 1926 ---, 1928 ——, 1931 -·-·-.

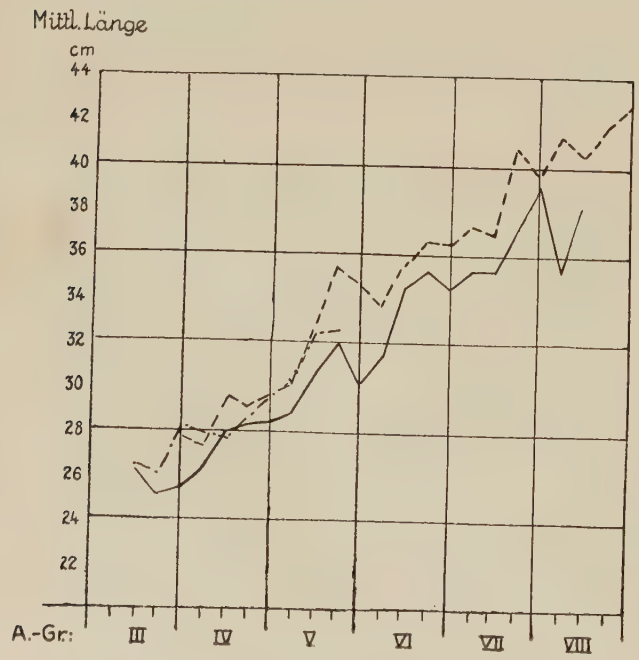


Fig. 9: Schollen ♀, Jahrgang 1927 ---, 1929 ——, 1932 -·-·-.

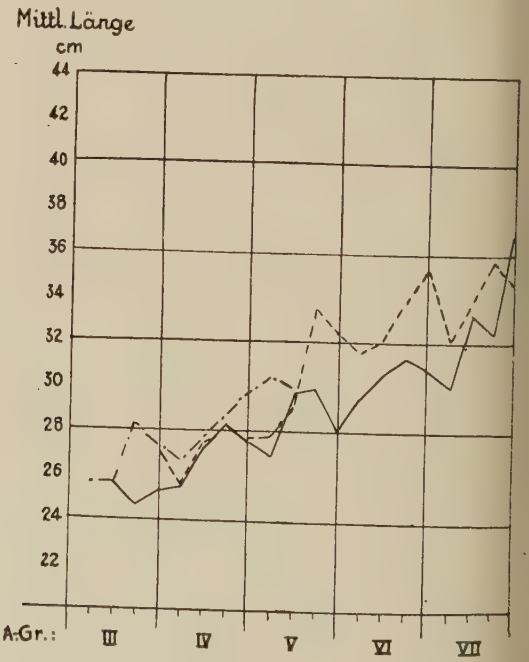


Fig. 10: Schollen ♂, Jahrgang 1927 ---, 1929 ——, 1932 -·-·-.

Fig. 7—10: Durchschnittslängen der in Grimsby gelandeten Schollen verschiedener Jahrgänge im Juni, September, Dezember und März aufeinanderfolgender Jahre.

kmann führt diese Unterschiede auf ankungen in der Wachstumsgeschwindigkeit k und weist nach, dass diese mit der Dichte Schollenbevölkerung in Zusammenhang stehen. Jahrgänge, die in Perioden dichter Bevölkerung nwachsen, haben langsames Wachstum, die, die erioden spärlicher Bevölkerung heranwachsen, elles. In dem Gebiet vor der holländischen e kommen auch Schwankungen in der Durchttslänge der Altersgruppen vor. Aber weder rsby-Pelham noch Bückmann und thaus konnten hier eine Beziehung zu der te der Bevölkerung erkennen. Die letztgenannAutoren vermuten, dass Einwanderungen heransender Schollen von der Deutschen Bucht her gen, die die Durchschnittslängen der Schollen er holländischen Küste stark beinflussen. Die nde Jensens über das Wachstum der Scholm Hornsriffgebiet stimmen dagegen mit denen kmanns und seiner Mitarbeiter aus der schen Bucht gut überein.

n der Deutschen Bucht waren 1929/30 Jahre h Wachstums, 1931/32 Jahre schlechten Wachs. Auf Grund der englischen Markierungsrimente kommt Hickling zu dem Schluss: no one year was there a more rapid growth at tations than in any other year." Doch vermag Feststellung das Vorkommen von Wachstumsankungen m. E. nicht zu widerlegen. Aus der Hickling mitgeteilten Tabelle ergeben sich nde Werte für den durchschnittlichen Jahreschs:

iet:	Hornsriff—Helgoland	Borkum—Haaks
—30	4·1 cm. (70 St.)	3·7 cm. (90 St.)
	4·2 cm. (184 St.)	2·7 cm. (20 St.)
	2·1 cm. (66 St.)	3·1 cm. (64 St.)

Nach unseren Feststellungen über die Durchttslänge gleicher Altersgruppen in verschiedeAbschnitten des Küstengebiets müssen wir hmen, dass die zum Markieren verwendeten llen im Borkum—Haaksgebiet jünger waren im Hornsriff—Helgoland—Gebiet. Es lassen Hicklings Befunde die Deutung zu, dass llen Gebieten ein Wachstumsrückgang eintrat, sich aber im Westen und Süden früher bemerkmachte als im Osten und Norden. — Die it Hicklings liegt dem Verf. z. Zt. noch vor. Weitere Prüfung dieser Frage müssen in Aussicht nehmen.

. Den Beweis dafür, dass die Unterschiede in mittleren Länge der verschiedenen Jahrgänge eine auf die Deutsche Bucht beschränkte heinung sind, liefern die von Thursbyham (MS.) mitgeteilten Befunde über die hschnittslängen der Altersgruppen in den llenanlandungen von Grimsby und Lowestoft. dem umfangsreichen Material geben wir die ramme Fig. 7—10 wieder, die dartun, dass so gut wie ausnahmslos die in Grimsby gelandeten Schollen der Jahrgänge 1926 und 1931 in gleichem Alter grösser waren als die des Jahrgangs 1928. und die Schollen der Jahrgänge 1927 und 1932 grösser als die des Jahrgangs 1929. Auf die Fehlerquellen, die die Durchschnittslängen der Altersgruppen in einem Marktmaterial beeinflussen, haben wir oben unter B hingewiesen. Die durchgehends gleichgerichteten Unterschiede in der mittleren Länge der genannten Jahrgänge sind aber garnicht anders zu erklären als durch Unterschiede in der Wachstumsgeschwindigkeit.

Thursby-Pelham hat dem mir freundlicherweise übergebenen Material eine Anzahl von Karten beigegeben, die Aufschluss über die Herkunft der in Grimsby und Lowestoft gelandeten Schollen geben. Es ist unmöglich, das ganze Material hier vorzulegen. Wir müssen uns mit der summarischen Feststellung begnügen, dass die Unterschiede in den Durchschnittslängen der verschiedenen Jahrgänge nicht durch verschiedene Lage der Fangplätze erklärt werden können, und dass die gelandeten Schollen nicht durchweg, ja nicht einmal vorwiegend aus der Deutschen Bucht und denjenigen tieferen Teilen der Nordsee stammen, deren Schollenbevölkerung von den Jungfischgründen der Deutschen Bucht kommt.

Es ist daher anzunehmen, dass die in der Deutschen Bucht beobachteten Wachstumsschwankungen in ähnlicher Weise in der ganzen südlichen Nordsee oder doch im grössten Teil dieses Gebiets aufgetreten sein müssen. Daneben gibt es nur die Möglichkeit, dass der in der Deutschen Bucht heranwachsende Nachwuchs für die Bevölkerung der ganzen südlichen Nordsee ausschlaggebend ist.

6. Bei dem gegenwärtigen Stande unserer Kenntnis können wir eine wohlbegründete Gesamtdarstellung des Wachstums der Schollen in der südlichen Nordsee noch nicht geben. Unsere Fig. 11 stellt nur einen Versuch dar, bei dem dem persönlichen Ermessen weitgehend Raum gegeben wurde.

V. Kliesche *(Pleuronectes limanda).*

Über die Wachstumsverhältnisse der Kliesche berichtet Aage J. C. Jensen in diesem Band, Beitrag Nr. 16. Wir geben hier nur die wenigen sonstigen Bestimmungen wieder, die für diesen Fisch vorliegen. Sie finden sich bei Poulsen (l. c., vergl. S. 74), der die Durchschnittslängen im Hornsriffgebiet im Frühling aus wissenschaftlichen Fängen und Marktanlandungen (III-Gruppe und ältere) festgestellt hat, und bei Tesch (MS.). Teschs Angaben beziehen sich auf die Puf-Anlandungen des Winters 1924/25, also auf Fänge, die mit sehr engmaschigen Netzen gemacht und aus denen die grösseren marktfähigen Fische herausgelesen waren. Teschs Durchschnittslängen für die älteren Gruppen dürften daher zu niedrig,

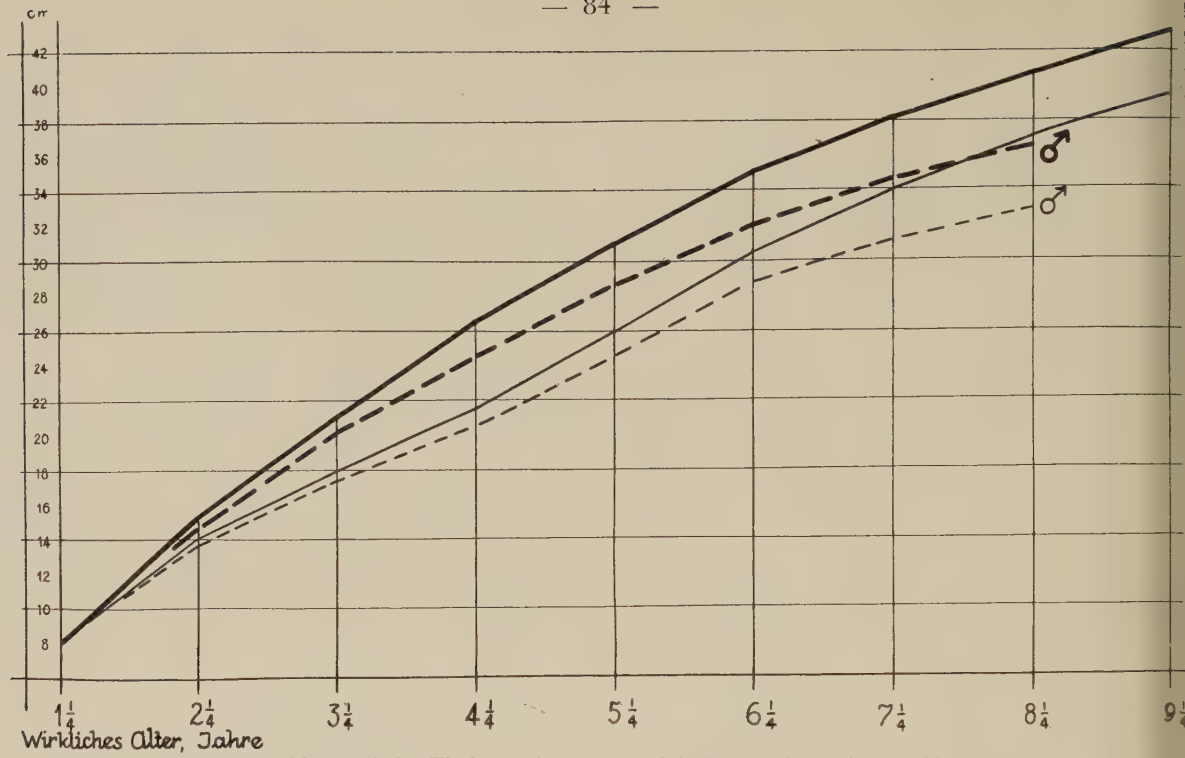


Fig. 11. Mutmassliche Wachstumskurven der Schollen in der südlichen Nordsee.
Fette Linien: gut gewachsene Jahrgänge. Ausgezogene Linien: ♀
Dünne Linien: schlecht gewachsene Jahrgänge. Gerissene Linien: ♂

Poulsens dagegen zu hoch sein. Zieht man dies in Betracht, so stimmen die Befunde recht gut überein:

	Altersgruppe I	II	III	IV	V	VI	VII
Poulsen							
Frühling							
Hornsriff	4	9	15	22	24	26	27
W. Limfjord ..	5	11	17	—	—	—	—
Tesch							
Winter							
Holl. Küste ...	13	15	18	—	—	—	—

VI. Seezunge *(Solea vulgaris)*

Über diesen Fisch liegen aus neuerer Zeit ausschliesslich die Untersuchungen von Bückmann vor. Sie sind ergänzt worden, soweit deutscherseits bearbeitetes Material aus den Jahren 1934—36 vorlag. Eine wesentliche Änderung unserer Vorstellungen über das Wachstum der Seezunge in der Nordsee ergibt sich aus diesen Ergänzungen nicht. Eine Wachstumskurve für die südöstliche Nordsee, beruhend auf den in den Frühjahrsmonaten beobachteten Durchschnittslängen, ist in Fig. 12 wiedergegeben. Es geht daraus hervor, dass die ♂ langsamer wachsen und kleiner bleiben als die ♀. Schwankungen des Wachstums sind bisher nicht festgestellt worden, doch ist das Material nicht so umfangreich, dass das Vorkommen solcher Schwankungen mit Sicherheit auszuschliessen wäre.

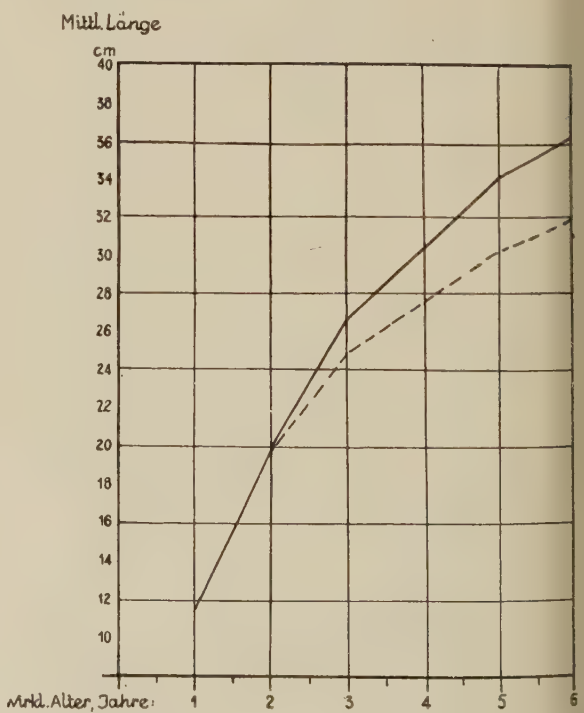


Fig. 12. Wachstum der Seezunge in der südöstlichen Nordsee.

13

AN INVESTIGATION INTO THE ALTERATIONS IN THE GROWTH-RATE OF THE HADDOCK

BY

K. A. ANDERSSON.

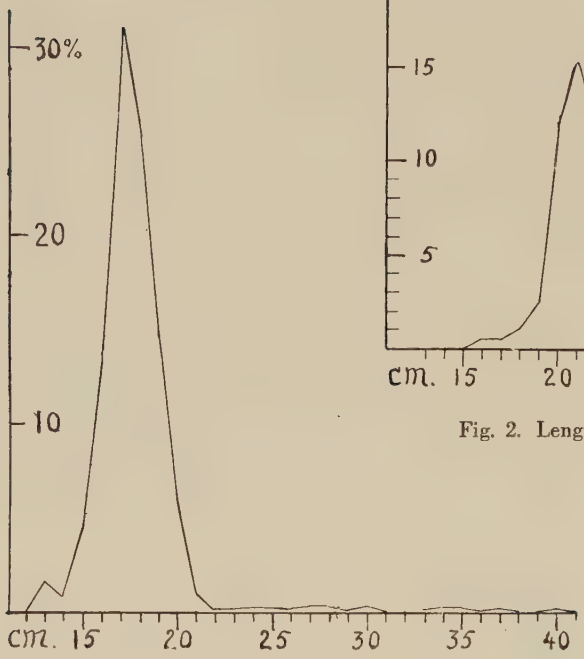


Fig. 1. Length curve of haddock from three hauls, 6th and 8th February 1929.

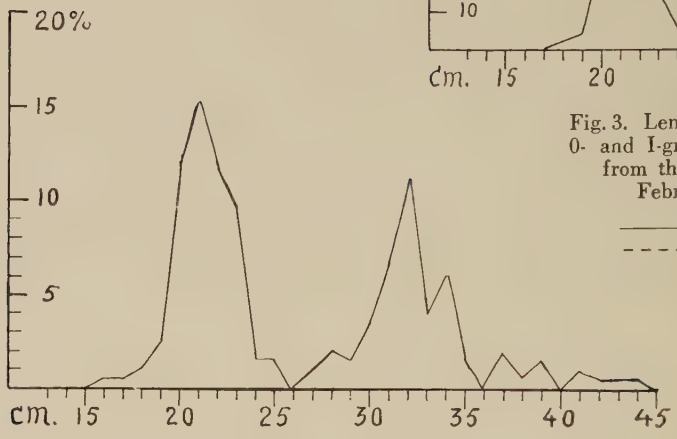


Fig. 2. Length curve of haddock from three hauls, 9th February 1938.

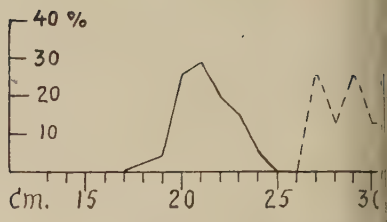


Fig. 3. Length curves o 0- and I-groups of had from three hauls, 9t February 1938.

——— 0-group;
- - - - I-group.

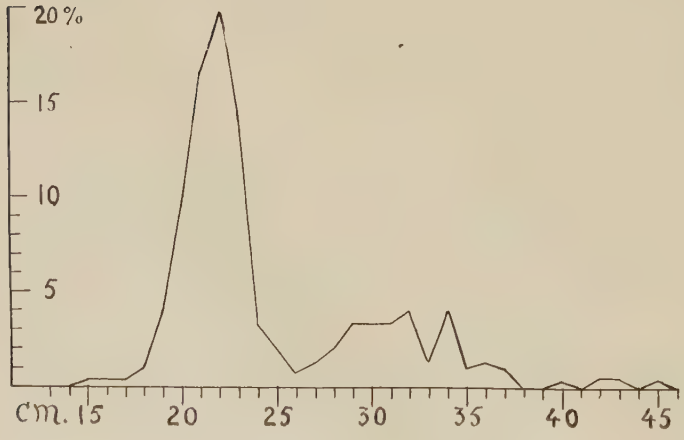


Fig. 4. Length curve of haddock from three hauls, 7th March 1938.

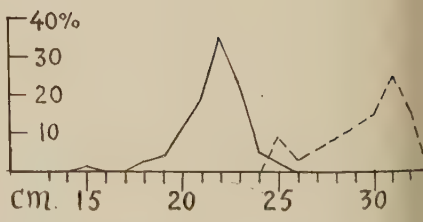


Fig. 5. Length curves of the 0- and I-groups of hadd from two hauls, 7th March 1938.

———0-group; - - - -I-group.

HADDOCK spawning in the Skagerak is as a rule so infrequent as to be of little significance. The stock of haddock in that sea therefore maintained, for the greater part, by the drifting of eggs and larvae from the North Sea into the Skagerak. The strength of the year-classes in the Skagerak depends upon their strength in the North Sea. Thus a large number of the eggs and larvae of the strong year-class 1928 drifted into the Skagerak and in February and March 1929 the I-group was extremely abundant there.

On Fig. 1 is given a length-curve of the total catch obtained in three hauls with a fine-meshed herring trawl on the 6th and the 8th of February 1929. A determination of age showed that the I-group had for the greater part a length of 18—19 cm.

Repeated age determinations made in March 1929 gave the same results. During a trawling operation carried out on 9th February 1938 with a fine-meshed herring trawl approximately in the same area (NW. of the Skaw) I was very surprised to find, when measuring the catch of haddock, that the length-curve was that given on Fig. 2. The I-group, according to this curve, ought to have a length of 20—23 cm., that is to say about 3 cm. longer than in 1929. An age determination of the material collected did indeed show that the 0-group had in the main a length of 20—23 cm. (Fig. 3).

The catches yielded by three hauls, on 7th March, approximately in the same area, showed the length composition given by Fig. 4. An age determination showed also here that the 0-group chiefly had a length of 20—23 cm. (Fig. 5).

Determinations of age compositions carried out on haddock from the same hauls of 7th March 1938 showed that also the I-group was considerably larger than normal (Fig. 5).

What can be the cause of this strong increase in the growth-rate of the haddock? A tempting explanation would be to seek its cause in some increase in the temperature of the bottom water. In the area of the Skagerak where this research upon the haddock has been carried out changes in the temperature occur fairly often. For that reason it is difficult to prove that the temperature has been above normal for any considerable part of the haddock's period of growth. I have, unfortunately, not had the opportunity of studying the question more closely.

It has, however, been easy to establish that there is a great difference between the abundance of the stock of the year 1929 and that of the year 1938.

Thus on 6th February 1929, NW. of the Skaw (Lat. 57°59′, Long. 9°50′), in a haul which lasted two hours with a fine-meshed herring trawl at a depth of 105—109 m. 23,750 specimens were obtained, 23,500 of which belonged the 0-group (nearly one year old). In five hauls in February and March 1929 the catch averaged 3,180 fish per hour, about 3,100 of which belonged to the 0-group. The total number per hour varied between 11,875 and 642 and the number of 0-group fish between 11,750 and 628.

In two short papers I have dealt with this matter[1]).

There is a striking contrast between these figures and those obtained from the catches made in February and March 1938. In six hauls with a fine-meshed herring trawl in the same area NW. of the Skaw in these months an average of 130 haddock per hour were obtained, 82 of which belonged to the 0-group. The total number varied between 42 and 250 and the number belonging to the 0-group between 12 and 165. The figures given above show that the density of the haddock stock in the examined area in 1929 was when regarding the whole haddock stock about 24 times. and when regarding the 0-group about 37 times larger than in 1938. This means that every haddock had in 1938 a 24 times larger area at its disposal than in 1929. As the haddock feeds on bottom animals (Cumacea, gammarids, annelids etc.) the above-mentioned conditions should have a great effect upon the haddock's thriving and upon its growth-rate. Scottish scientists have also proved that the haddock has different growth-rates in different areas[2]). Poulsen has reported that the haddock exhibit a higher growth-rate in the Belt Sea than in the North Sea[3]). The conditions described regarding the Skagerak in 1929 and 1938 show clearly that the growth-rate can vary considerably in the same area. It seems highly probable that this depends upon the various densities of the stock, and therefore upon the different supplies of food per specimen. One may venture to say that in 1929 a state of overpopulation and in 1938 a state of "underpopulation" existed in the area mentioned and that this is the reason why haddock of 0-group and I-group were larger in 1938 than in 1929.

---

[1]) K. A. Andersson in "Ny Svensk Fiskeritidsskrift" 1929, No. 8 and 1931, No. 19.

[2]) See Ritchie, A., The food and feeding habits of the Haddock (*Gadus aeglefinus*) in Scottish waters. Fisheries, Scotland, Sci. Invest., 1937, No. II.

[3]) Poulsen, Erik M., The Haddock of the Belt Sea and Western Baltic during the Years 1926—1928. Rep. Dan. Biol. Stat., XXXIV, 1928.

14

NVESTIGATIONS INTO THE GROWTH-RATES OF HE COMMON DAB AND THE FLOUNDER IN THE SOUTHERN BALTIC

BY

ARVID R. MOLANDER

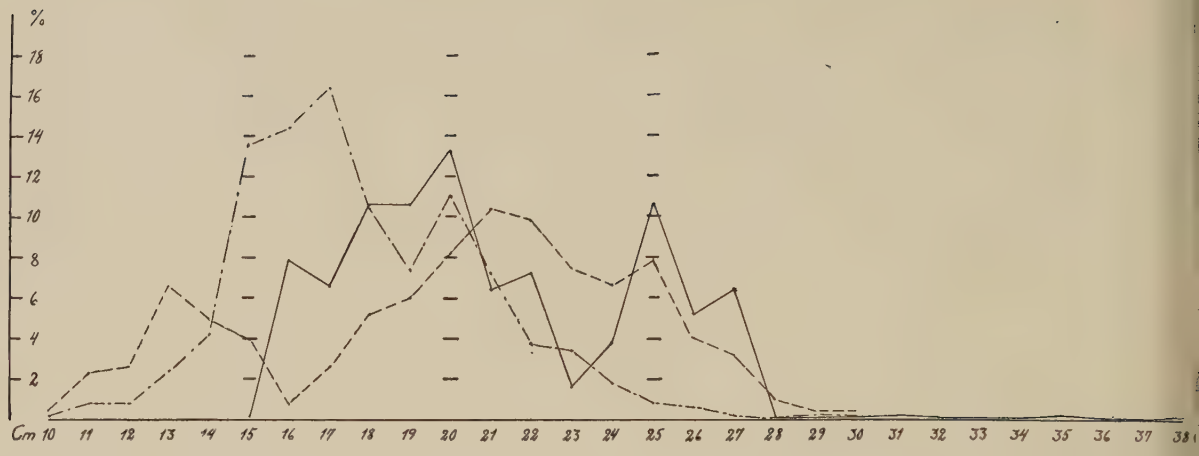


Fig. 1. Length curves of the Common Dab from the Bornholm area and off the south coast of Scania.
—·—·—· Sept. 1921 (S 5). — — — — Oct. 1927 (S II, S VIII). ———— Sept. 1937 (Y III, Y X).
Positions of the stations: See Molander: Svenska Hydrogr.-Biolog. Komm. Skrifter, N.S., Biologi, Bd. I, No. 1, Tab. 1 and the chart.

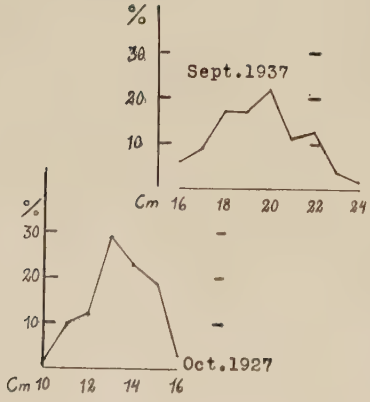


Fig. 2. II-Group.

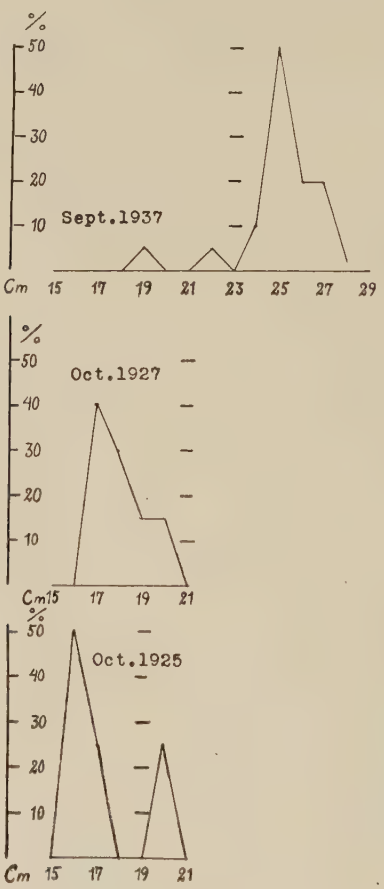


Fig. 3. III-Group.

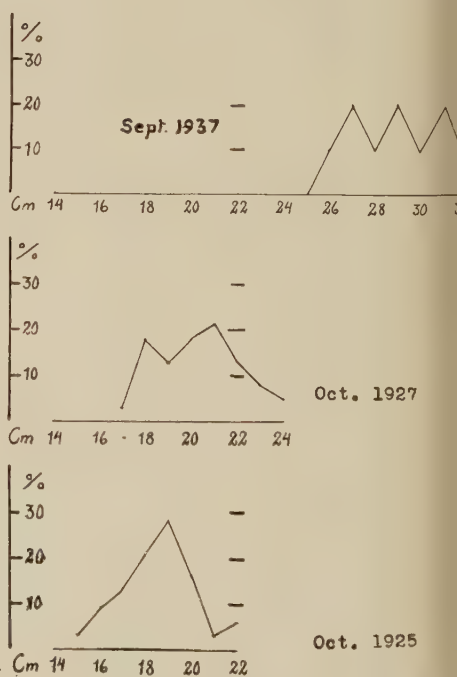


Fig. 4. IV-Group.

Figs. 2—4. Length Curves of the Common Dab.

I. The Common Dab.

AN examination of the length of common dab from the southern Baltic shows a strong increase in its average size from the time before trawl-fishing started there (1921) and onwards. It may be seen from Fig. 1 that the number of larger specimens has considerably increased and this was already distinctly noticeable in 1927. The increase in the average size and in the number of larger specimens has continued up to recent years (1937), as the length curves of Fig. 1 indicate. The average size for 1921 is 17·8 cm., for 1927 20·0 cm., and for 1937 21·6 cm.

If we go on examining the distribution of the length-classes of the common dab within their respective age-groups, we see to how high a degree the length of the common dab has increased during the above-mentioned period. On Fig. 2 I have established the curves indicating the distribution of length-classes within the age-group II. The curves show that in October 1927 specimens, between 10 and 16 cm. long, belonged to it. The vertex of the curve is situated at 13 cm. In September 1937, the sizes of the common dab of group II varied between 16 and 24 cm. and the vertex of the curve is

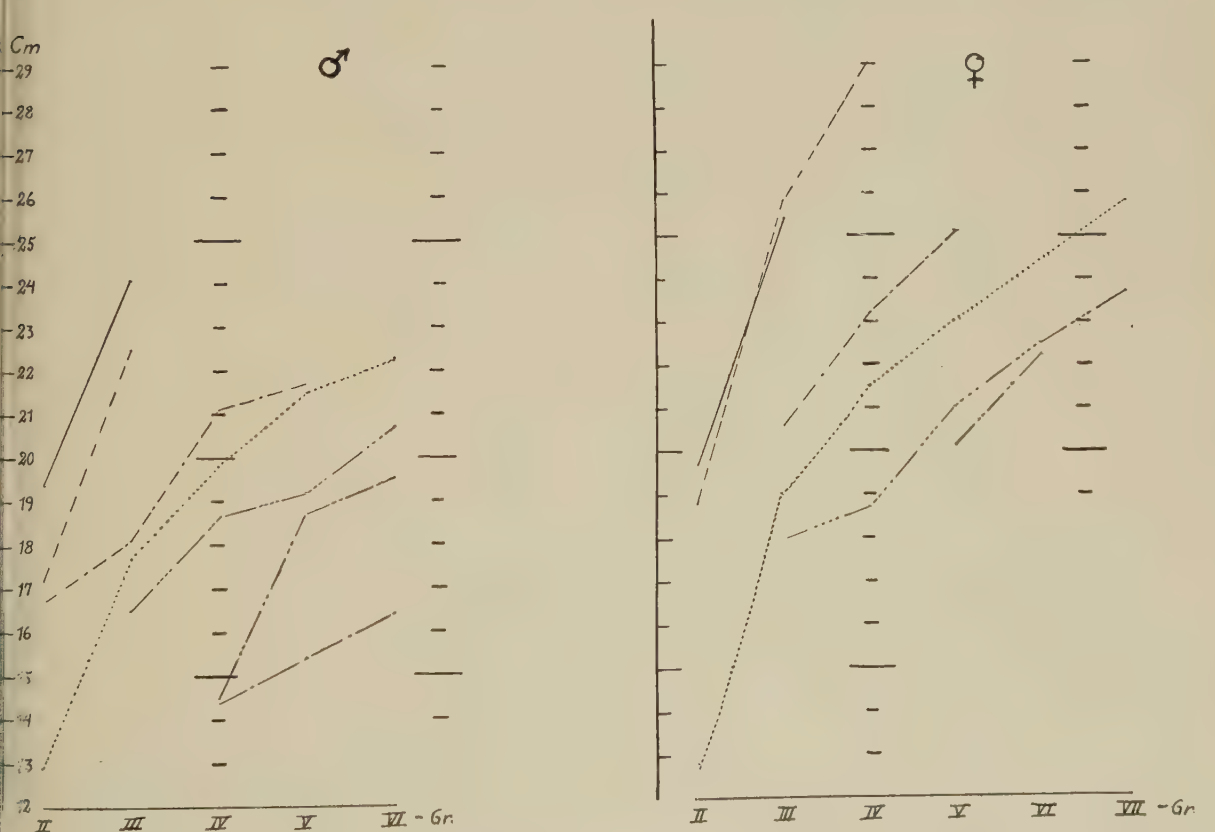


Fig. 5. Average length of the II—VII-groups of the Common Dab in the Southern Baltic 1919—1937.
— · · — June 1919 (Y IV). — · — July 1919 (Gothland). — · · · · — Oct. 1925 (Y X). · · · · · Oct. 1927 (S II, S VIII).
— — · — — Oct. 1931 (S IX). — — — — Sept. 1935 (S VIII). ———— Sept. 1937 (Y X).

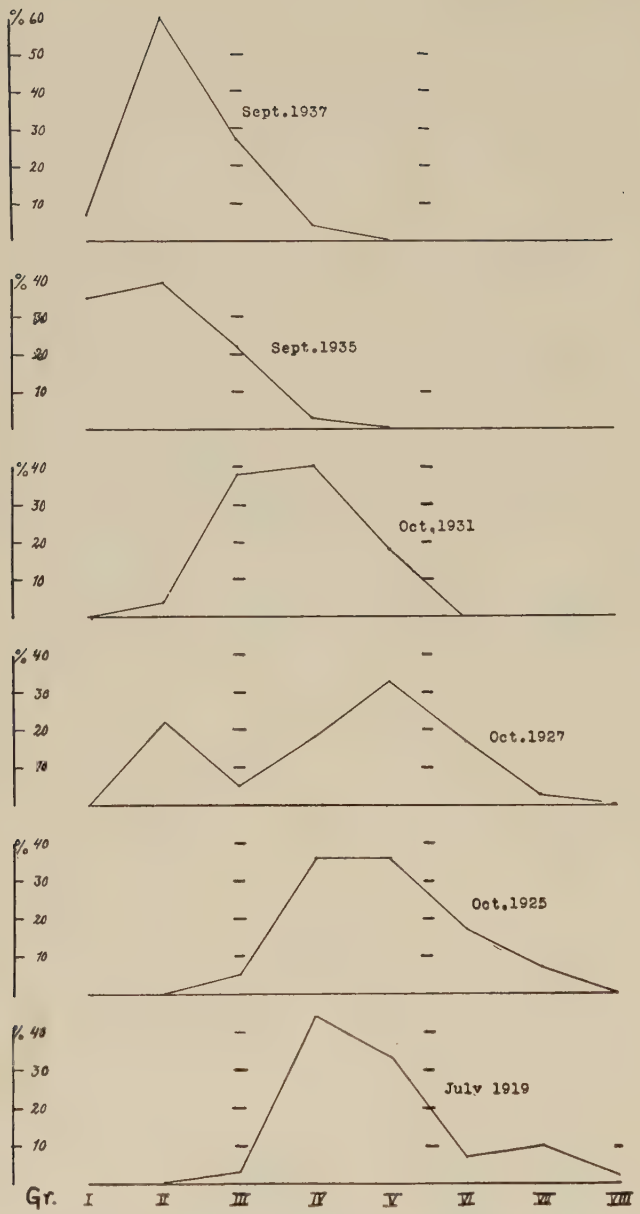


Fig. 6. Curves of the year-groups of the Common Dab in the southern Baltic, 1919—1937.

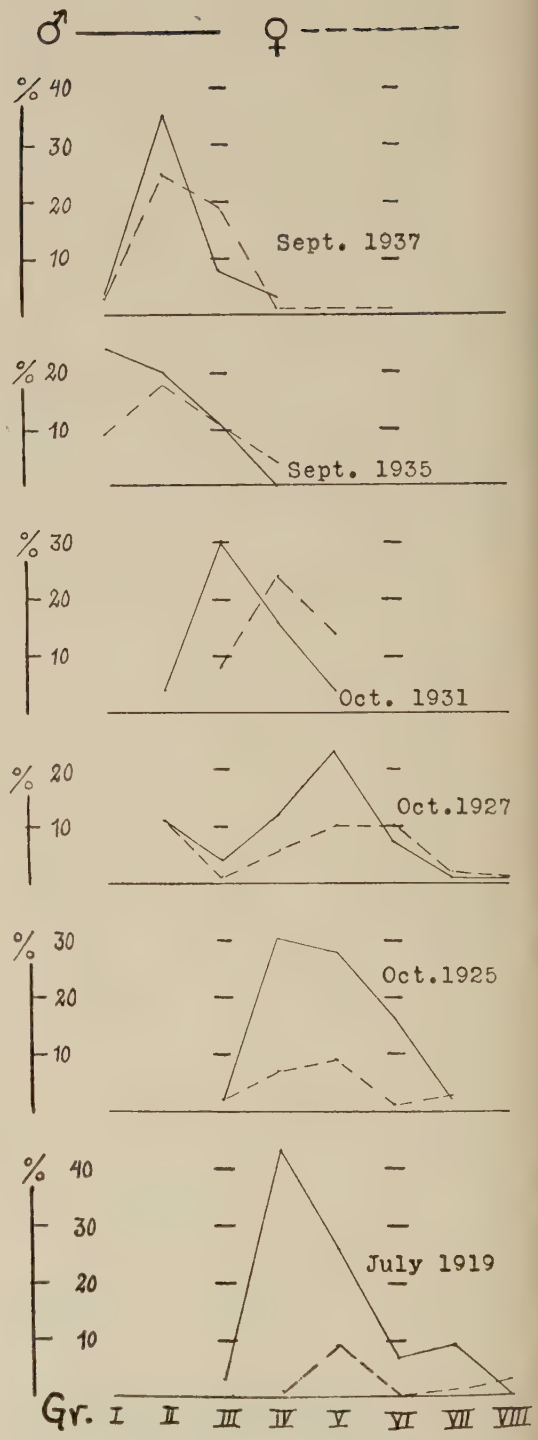


Fig. 7. Frequency curves of males (♂) and females (♀) of the Common Dab, 1919—1937.

situated at 20 cm. Similar remarkable changes tending towards a greater length were also noticed in specimens belonging to groups III and IV (Fig. 3—4). Particularly pronounced is the change that took place from 1927 to 1937.

On Fig. 5 are drawn the curves indicating the rate of growth of the common dab, both males and females, for different years. The age determination according to which the curves of the rate of growth were established, were made on common dabs from the years 1925, 1927, 1931, 1935, and 1937. The

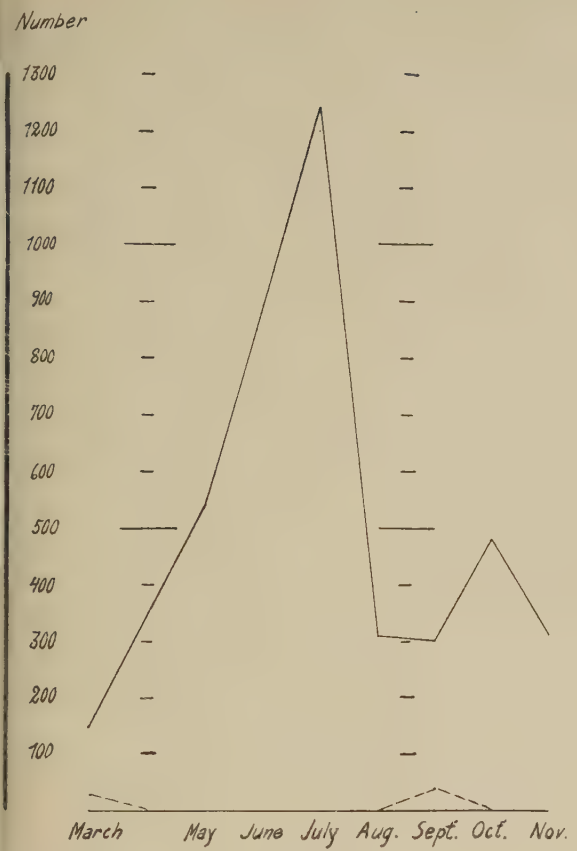


Fig. 8. Catches of Common Dab per trawling hour during March—November 1913—1923 ———— and in March and September 1937 in the Bornholm area and off the south coast of Scania. — — — —

samples were collected in September or October and were obtained by trawling in the deep area north and east of Bornholm and between Ystad and Rügen. Fish caught in herring trawl or in fine-meshed otter seine furnished the samples. For comparison's sake another curve has been drawn, indicating the rate of growth of common dab caught in July 1919, according to Hessle (Medd. från Kungl. Lantbruksstyrelsen, No. 243, 1923). Fig. 5 shows a somewhat higher rate of growth of the females (cf. E. M. Poulsen, Ber. Dan. Biol. Stat., XXXVIII, 1933). Further it is seen very clearly that the rate of growth of the common dab has strongly increased from 1919 to 1937. The rate of growth of the common dab in the southern Baltic is now higher than that indicated by Poulsen (*loc. cit.*) regarding common dab from the Kattegat. The rate of growth has been increasing steadily and continuously during the years in which research work has been carried out. It is indeed a particularly striking change that has taken place during those years regarding the rate of growth of the common dab. It implies at the same time a very significant improvement of the quality of the stock.

Corresponding with this alteration in the rate of growth we also find certain other features which can be said to characterize a fish stock in which the rate of growth of the specimens increases rapidly. It is above all the relation between the strengths of the different year-classes that alters considerably. In 1919 the stock consisted chiefly of older common dabs of the year-groups IV—VII (Fig. 6). This age distribution still prevailed on the whole in 1925 and 1927. In 1931 the presence of a considerably larger proportion of younger year-classes became manifest (groups III—IV). In

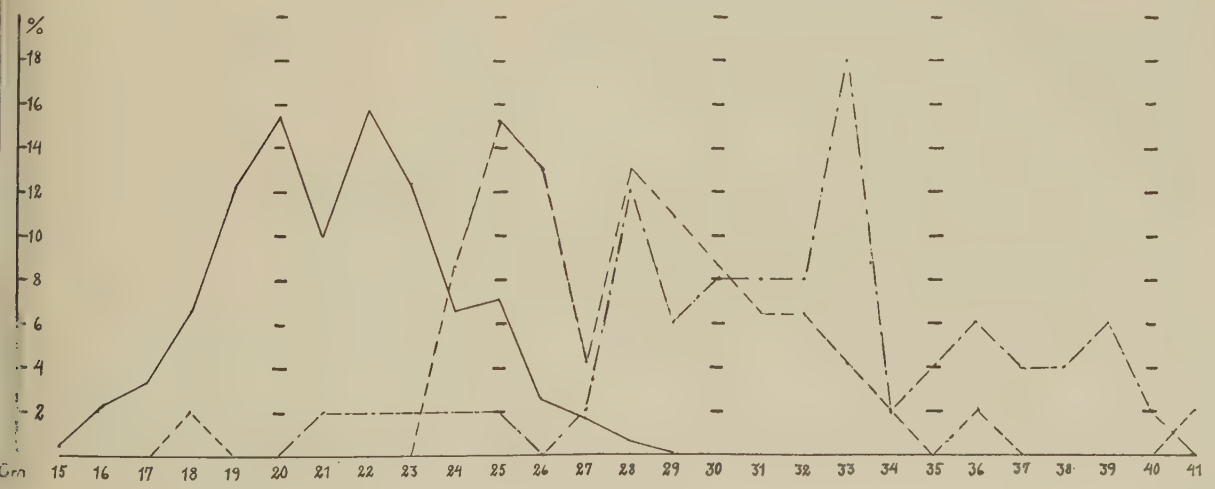


Fig. 9. Length curves of Flounder from the Bornholm area.
———— May 1916 (S II). ···· Feb. 1930 (C VII). —·—·— March 1937 (SO IV).

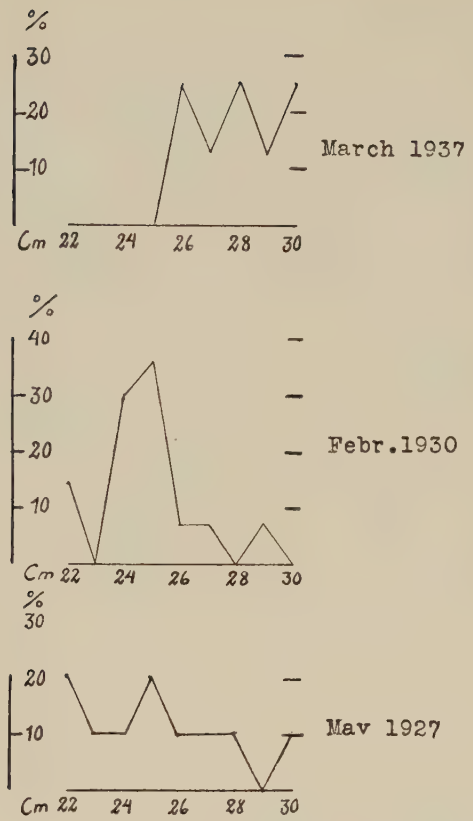


Fig. 10. Length curves of the IV-group of the Flounder.

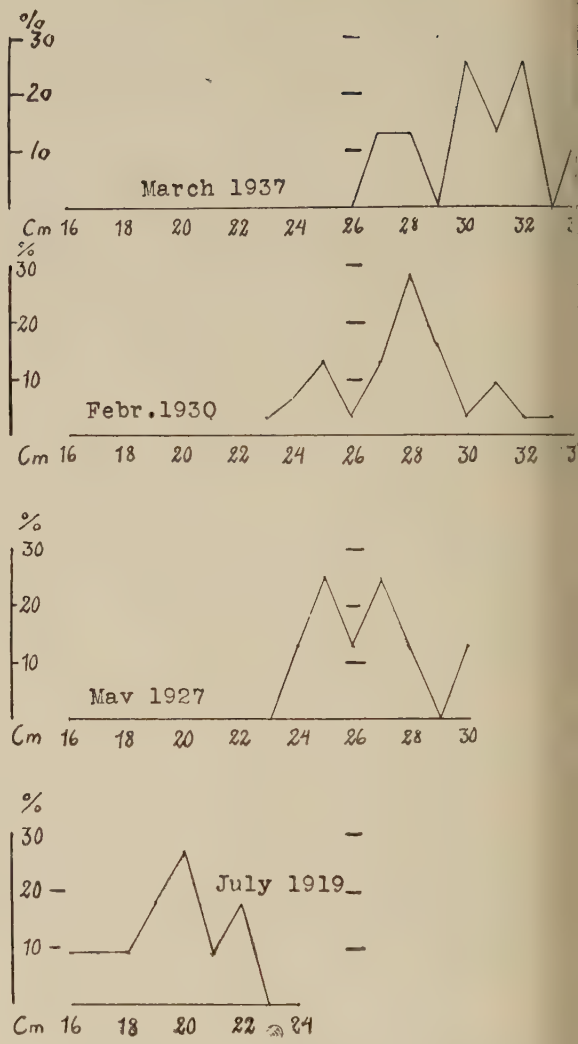
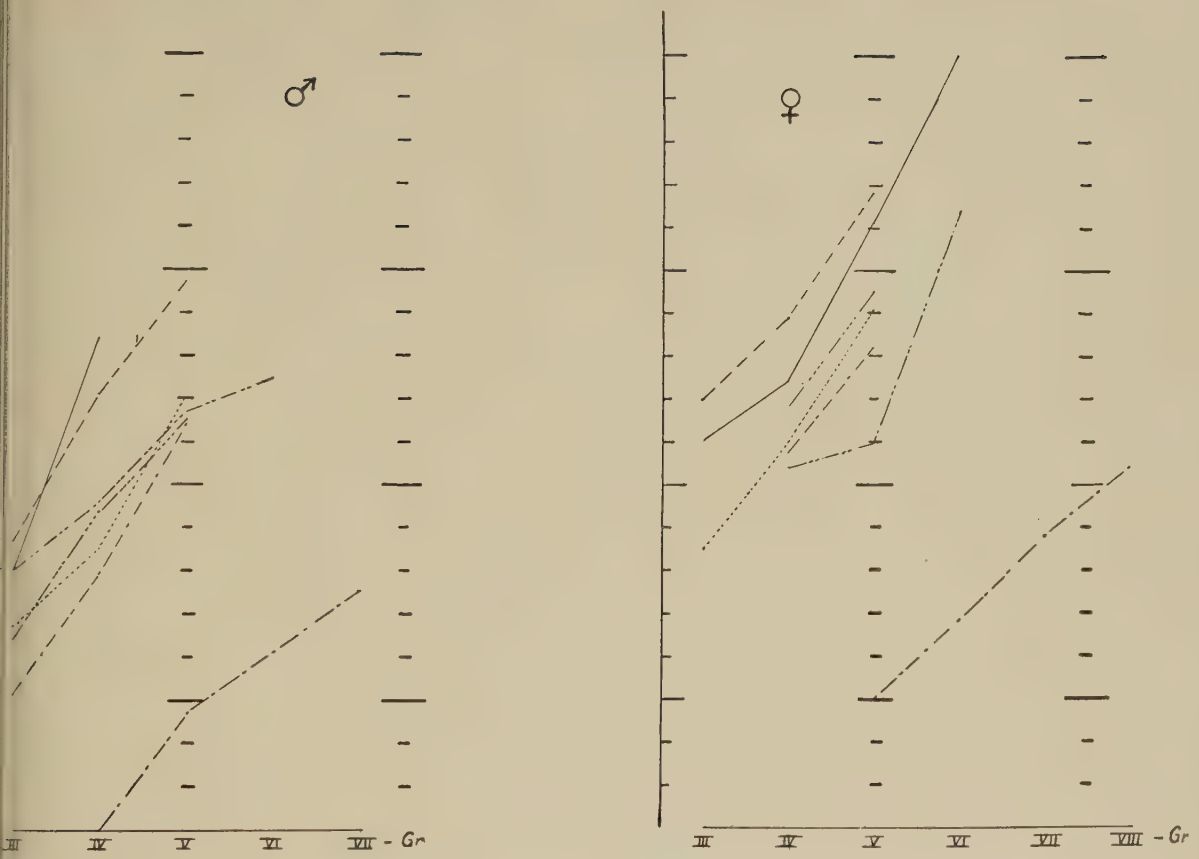


Fig. 11. Length curves of the V-group of the Flounder.

1935—1937 group II was predominant together with a not inconsiderable portion of group I. The older groups simultaneously disappeared more and more from the catches. It is interesting, too, to note in the same connexion that the numerical relation of males to females has also undergone a change. Formerly males outnumbered females even within the age-groups VII and VIII (Fig. 7). But concurrently with the increased rate of growth and the regrouping of the year-classes within the stock, the males' numerical superiority has become more and more confined to the younger year-classes while the females have correspondingly begun to preponderate more and more. Among the older fish females now always outnumber males. The strong decrease in numbers of the older males is especially characteristic and might well be closely connected with the strongly increased rate of growth. Thus in 1919 the average length of a 6-year-old male was 16·5 cm.; in 1937 a 2-year-old male was, on the average, nearly 19·5 cm. long. In 1937 4-year-old males reached a length of 27—29 cm.; in 1919 only 8-year-old or even still older females reached such a length. The males, therefore, do not appear to grow beyond a certain length and the life of a male seems to be shortened proportionately with the increase in the speed with which this length is attained.

The explanation of this marked increase in the rate of growth of the common dab is, of course, to be sought in the striking thinning out of the stock which was the consequence of the large-scale fishing carried out in the southern Baltic. A thinning out of the stock and the increased rate of growth that followed have already been pointed out by several authors with reference to the plaice and the flounder, and the examples here quoted point to similar conditions concerning the common dab. Fig. 8 shows the enormous difference between the



2a. Average length of the III—VIII-groups of the Flounder in the southern Baltic during the spring months 1919—1937.

—·—· July 1919 —··—·· May 1927 —····— Feb. 1930 — — ·— — — March 1931 ····· Feb. 1933.
— — — — March 1936 —— ——— March 1937

of the catches of the years 1913—1923 and e of 1937. An examination of common dab hes from the waters off Gothland in June 1919 e s s l e, *op. cit.* 1923) showed that the rate of vth of the common dab was far better there off the coast of Scania during the same period . 5). It was noticed at the same time that the mon dab was relatively rare near Gothland e it was very abundant in the area off Scania. n in this instance differences in the density of stock have obviously brought about different of growth, in correspondence with what has ened in recent years, but to a much higher ee, regarding the stock of the southern Baltic.

II. The Flounder.

In two papers (M o l a n d e r, Rapp. et Proc.-Verb., Vol. LXXVIII, 1932; Svenska Hydr. Biol Komm. Skr., N.S. Biologi, Bd. II, No. 1, 1937) I have dealt with the rate of growth of the flounder in the southern Baltic. The following report on this rate of growth is in the first place a summing up of the conclusions I had come to in the above-mentioned works, but it is also based upon research work carried out quite recently.

A comparison between the composition of the flounder stock in catches made with herring trawl in the southern Baltic, on the one hand before the large-scale fishing with drag-nets started there (May 1916), and on the other hand in more recent years (Feb. 1930, March 1931), shows that the

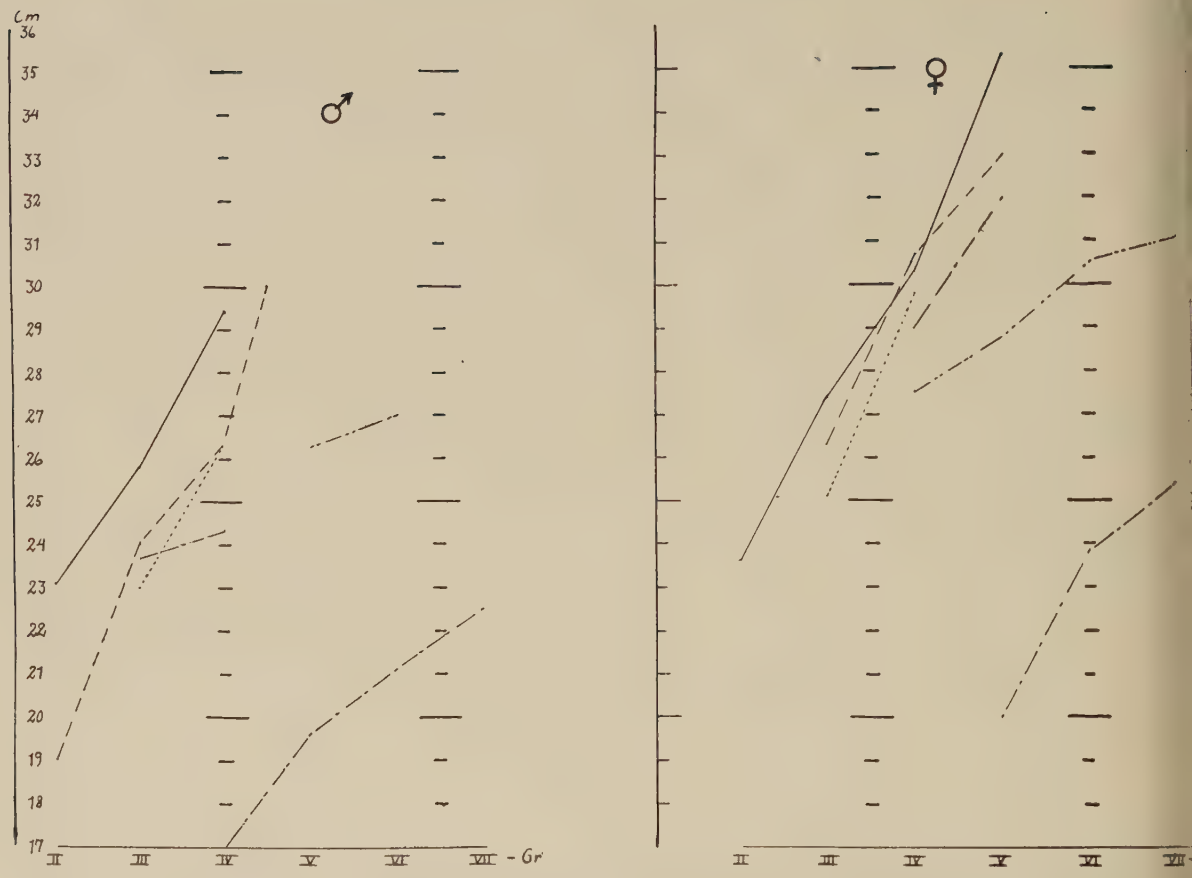


Fig. 12b. Average length of the II—VIII-groups of the Flounder in the southern Baltic during the autumn months 1919—19

—·—· July 1919 —·—·—· Oct. 1926 — — ·— — Oct. 1931 ····· Oct. 1932 — — — Sept. 1933 ——— Oct. 19

average size of the flounder (Fig. 9) has considerably increased. While the average size in the catch of May 1916 was only 21·2 cm., it was 28·2 cm. in February 1930 and 31·7 in March 1937. How this average increase in the size of the flounder is distributed within the different year-classes, may be gathered from Fig. 10—11, where I have established the curves of the distribution of the length classes in percentage within the age-groups IV and V. Within group IV (Fig. 10) the curve shows, for the year 1927, two peaks, one at 22 cm. and the other at 25 cm.; for 1930 the curve shows a peak at 25 cm., and for 1937 the maxima of the curve have moved to 26, 28, and 30 cm. As to group V (Fig. 11), the continuous movement towards the higher length-classes already observed in group IV, appears here too, perhaps still more clearly, especially if compared with the size of the flounder in 1919. The change tending towards a greater length within groups IV and V is not qu so pronounced between 1927 and 1930, but fr 1930 to 1937 on the other hand a very mark increase in the size of flounders has taken place

Fig. 12 indicates the average length of ma and females according to year-class, partly from spring months of 1927—1937 (Fig. 12a) and par from the autumn months of 1926—1935 (Fig. 12 In the same figure I have also drawn a curve the average length of the flounder in a sam from July 1919. All the samples examined co from the areas situated north and east of Bornho and off the south coast of Sweden, which regularly visited by Swedish fishermen (cf. M l a·n d e r, Rapp. et Proc.-Verb., Vol. LXXV 1932). They were obtained by fishing with herring trawl or a fine-meshed otter seine (19 1937).

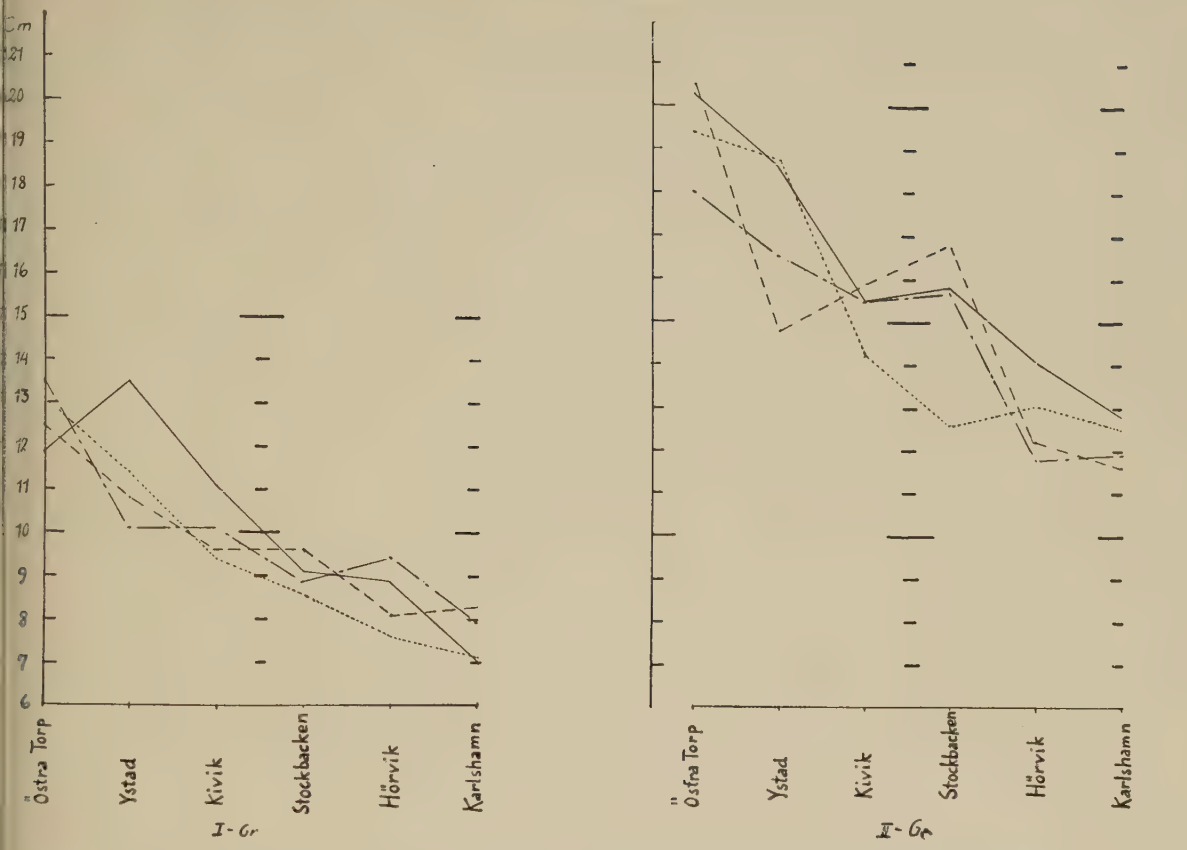


Fig. 13. Average length of the I—II-groups of the Flounder in the Swedish coastal area.
····· 1933 —·—·— 1934 — — — 1935 ——— 1937

Regarding the rate of growth of the flounder in above-mentioned area we notice in the first ce that it is considerably higher as regards the nales. Further there appears to have been a rticularly strong increase in the rate of growth m 1919 to 1926 or 1927. During the years that lowed until the beginning of the thirties the rease has not kept up the same pace, and both ing and autumn samples show a relatively small nge in the average size within the age-groups mined. During the most recent years (1936—37) a fresh increase in the rate of growth seems vever to have taken place. It appears especially samples collected in spring months (Fig: 12a). The examples of the rate of growth of the nder in the southern Baltic which are given on . 12 are all taken from material obtained within deep areas where fishing with trawl and otter ne is practiced. It is, however, also interesting follow the rate of growth of the young year-sses which preferably keep to the shallow water in the coastal area. Fig. 13 shows the average length of the flounder groups I and II from a number of stations along the coasts of Scania and Blekinge. It is not possible to find here any variations in the rate of growth worth mentioning, nor is it possible to observe any increase in the rate of growth during the above-mentioned years.

On the other hand the curves show a very clear decrease in the rate of growth of the flounder from the western stations of the Scanian coast (Östra Torp, Ystad) to stations on the east coast of Scania (Kivik, Stockbacken) or in Blekinge (Hörvik, Karlshamn).

Even if other factors, governing the rate of growth of the flounder, than those existing in deep areas are probably at work in coastal areas, it is nevertheless possible to prove by examples taken from catches made in the coastal waters that a definite correlation exists between the size of the stock and the rate of growth of the flounder (Fig. 14).

Fig. 14. Average length of the I-group of the Flounder in the coastal area off Ystad and Karlshamn ————. Number of specimens per 30 minutes trawling — — — —

Examples taken from Ystad and Karlshamn where the catches of younger flounders are usually good actually show that in the years when the catches are large the average size of the captured flounders is lower.

At the same time as this altered rate of growth manifests itself within the flounder stock of the southern Baltic, we also come across certain other features which often characterize a fish stock in which the rate of growth of the specimens is strongly increased(Fig. 15). Thus on Fig. 15 we see that the strength of the older year-classes has gradually decreased in the course of years and that the stock at present is chiefly recruited from the younger year-classes (III and IV). That the still younger year-classes do not appear is caused by the fact that they are not caught by the usual fishing implements. In this respect too a certain stabilization has taken place recently (1925—1937). We notice at the same time that a change takes place in the occurrence of males and females within the year-classes. During former years the males were strongly preponderant in spring-month catches (Fig. 16). In autumn when the stock of flounder in deeper areas is always smaller the females on the other hand seem, as a rule, to have been preponderant. But concurrently with the change in the rate of growth and the decrease in the older year-classes, the predominating proportion of males has gone over to the younger year-classes in which the females themselves appear more frequently than before. Among the older specimens (group V and older groups) females are now always preponderant and males have almost entirely disappeared. This disappearance of the older males has in all probability been caused by their strongly increased rate of growth, which again has caused them sooner to reach their maximum size.

The examples of alterations in the size and rate of growth of the flounder briefly described here must beyond all doubt be connected with the thinning out of the stock which has taken place as a result of the strongly increased fishing operations carried out in the southern Baltic. Fig. 17 shows to what extent the catches of flounder made during fishing experiments carried out onboard the research vessel "Skagerak" have decreased if we compare for instance the year 1922 with the years 1930, 1931, 1933, and 1937. The reduced landings of flounder in the harbours of Scania and Blekinge (M o l a n d e r, Sv. Hydr. Biol. Komm. Skr., N. S. Biologi, Bd. II, No. 1, 1937) point to the same

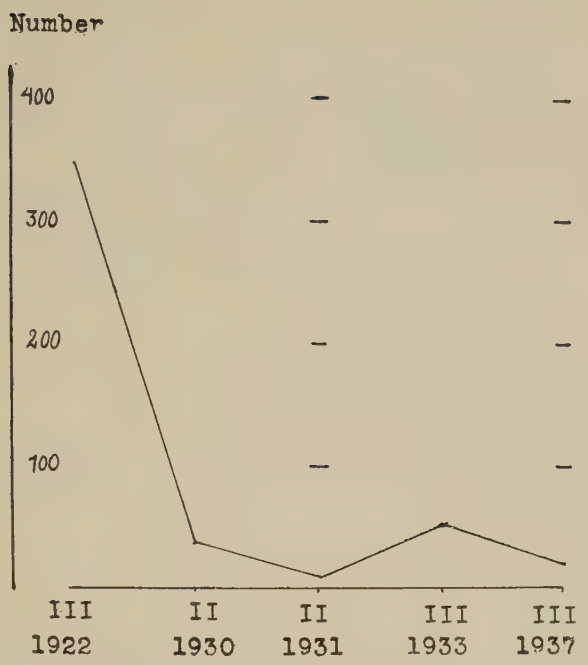


Fig. 17. Catches of Flounder per trawling hour (herring trawl) during Feb.—March 1922, 1930, 1931, 1933 and 1937 in the Bornholm area.

clusion. It is not, however, uninteresting to ord in this connexion that the rate of growth and o the distribution of the year-classes during ent years have become more and more stable, ch may possibly indicate that the thinning-out cess has reached the point at which it no longer rts any influence upon the rate of growth. Still, somewhat increased rate of growth of the nder observed during the last two years may icate that this thinning-out of the stock has not reached its extreme limit.

As to the rate of growth within the coastal area, the local differences I have pointed out are no doubt closely connected with varying physical conditions which consist above all in the continuous decrease in salinity from west to east. The stock may indeed become particularly dense at certain stations and in certain years, and in such cases the rate of growth may possibly suffer a strong local decrease, as shown on Fig. 14. Here, then, we come across the same conditions as were to be found in the overcrowded stock in deep waters. It shows incidentally how labile the rate of growth can be.

(Figs. 15 and 16: see page 100—101).

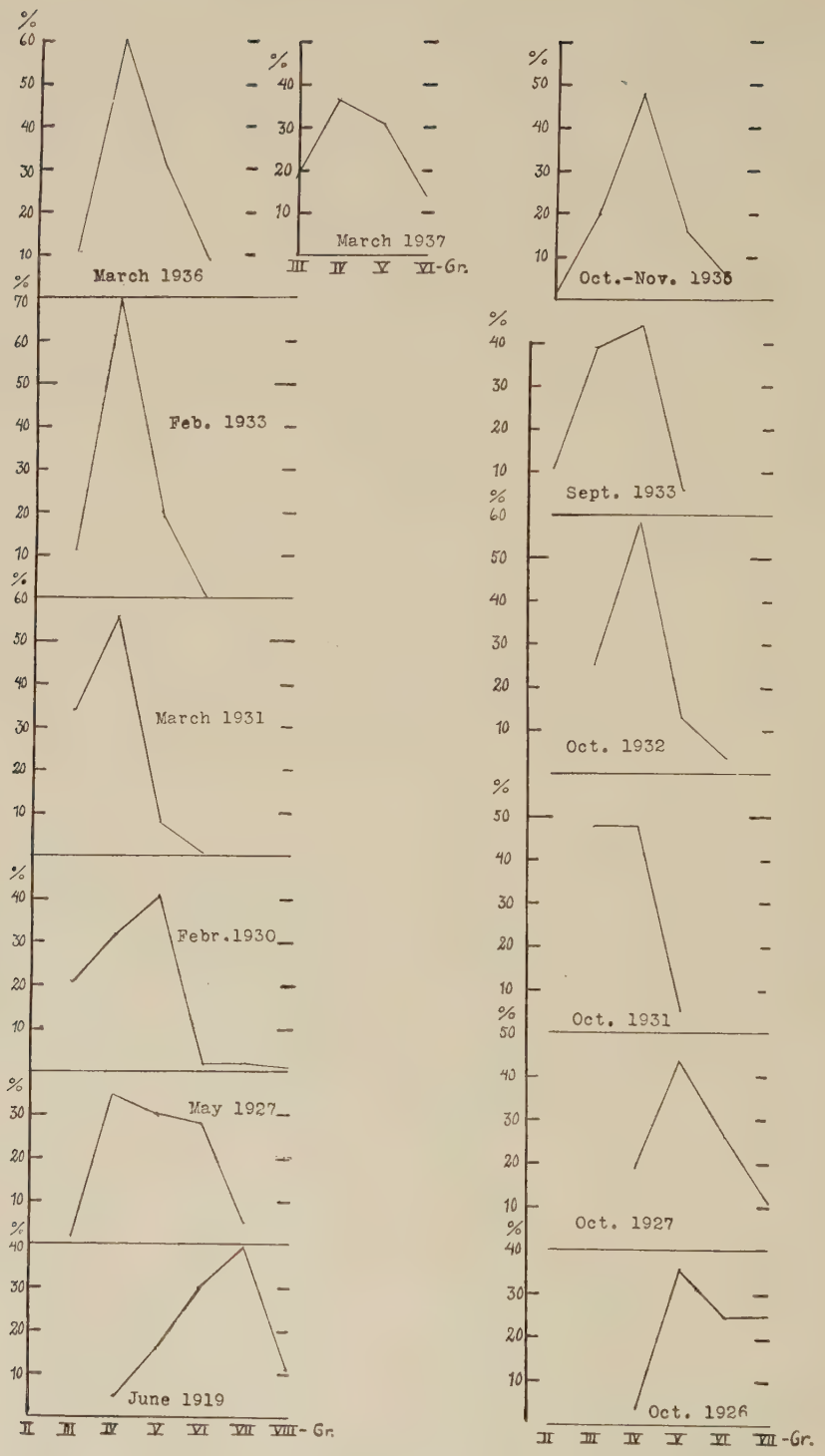


Fig. 15. Curves of the year-classes of the Flounder in the southern Baltic 1919—1937.

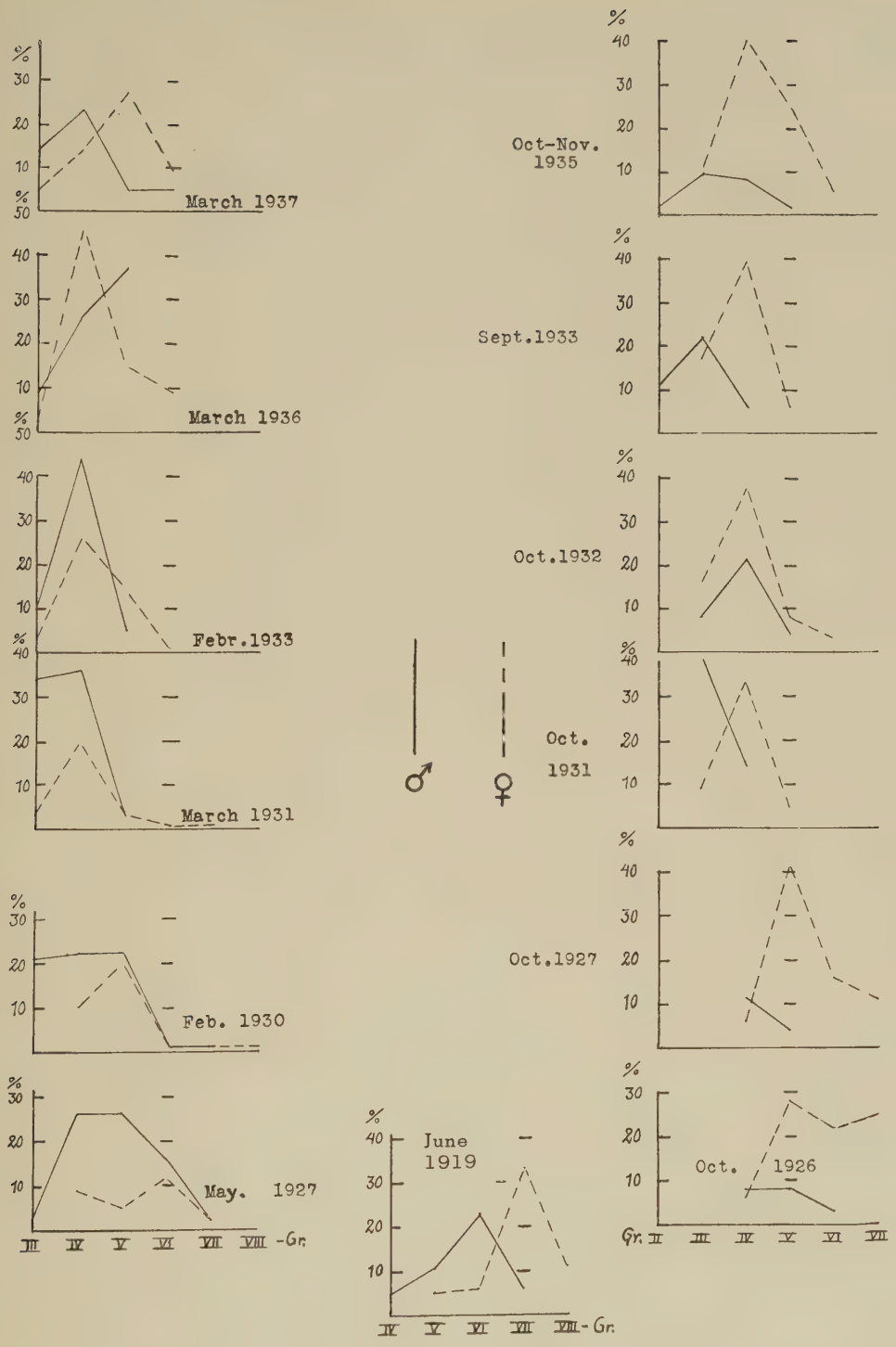


Fig. 16. Frequency curves of males (♂) and females (♀).

15

THE GROWTH OF THE PLAICE IN THE TRANSITION AREA

BY

AAGE J. C. JENSEN

THE length of the different age-groups within the stock in the sea is determined partly by the growth and partly by the effect of the fishery on the stock.

The effect of the fishery is considerable throughout the area. In marking experiments carried out during recent years about 50 % of the fish marked at a length of 20—25 cm. were recaptured in the course of the first year after the marking (according to H. Blegvad, 1934, p. 29[1])). It is therefore evident that a very considerable proportion of the plaice stock is removed by the fishery, but on account of the size limit none of the fish below about 26 cm. are taken.

When the plaice of a certain age-group reach the length at which the fastest growing individuals of the group begin to fall victim to the fishery — and the group thereby being perceptibly depleted — the average size of the remaining number will be correspondingly reduced. This reduction in the average size amounts in the Belt Sea to 2 cm. for the age-group which is just reaching the size limit (II-group). As regards the northern Kattegat where the fishery is equally intensive, but the growth slower, the reduction may be estimated to be about 1 cm.

For the Bohuslän Fjords Dr. Molander[9] has shown that the increase in length with increasing depth is very great.

The length of the age-groups during September—March was:—

	Gullmar Fjord		Stig Fjord
	5—9 m.	30—35 m.	7—25 m.
I-group	—	—	16·6 cm
II-group	—	—	23·4 cm
III-group	27·6 cm.	34·0 cm.	25·1 cm
IV-group	31·1 cm.	35·9 cm.	28·7 cm

In the Aalbæk Bay—Herthas Flak area the difference in length of an age-group between the corresponding depths was a few cm. only.

Molander states that the differences are due, to some extent, to the varying density of the stock, but for the Stig Fjord, for instance, the small lengths persist in spite of a very rich bottom fauna. Molander ascribes it to the comparatively low salinity of about 21—24 ‰. Yet the transplantations of plaice from the North Sea to the Belt Sea have shown that the North Sea plaice may thrive well at salinities as low as about 15 ‰, and it must be assumed that other factors — perhaps the temperature — contribute to the slow growth-rate recorded.

[1]) H. Blegvad, Transplantations of Plaice from the North Sea to the Belt Sea 1928—1933. Rep. Dan. Biol. Stat., XXXIX, 1934.

[9]) Arvid R. Molander: Investigations of Plaice off the West-Coast of Sweden. Rapp. et Proc.-Verb., Vol. LXXI, 1931, p. 77 et sequ.

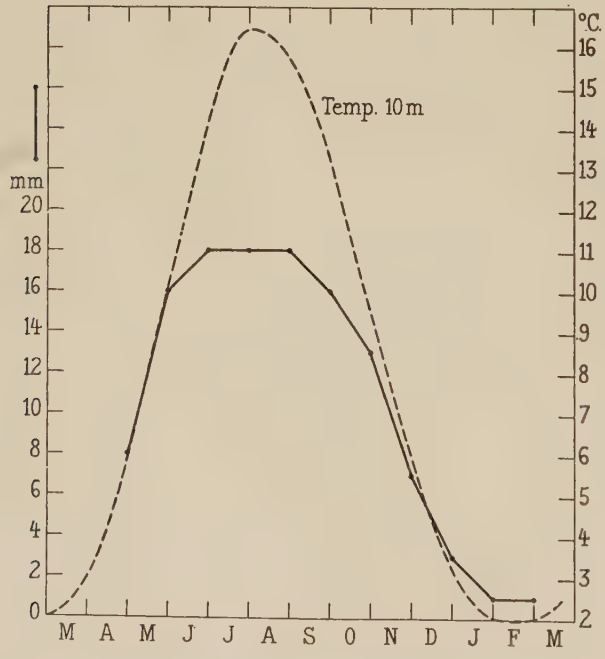


Fig. 1. Monthly growth of transplanted North Sea plaice in the Sejrø Bay compared with the mean temperature at "Schultz' Grund" L. V., 10 m. depth.

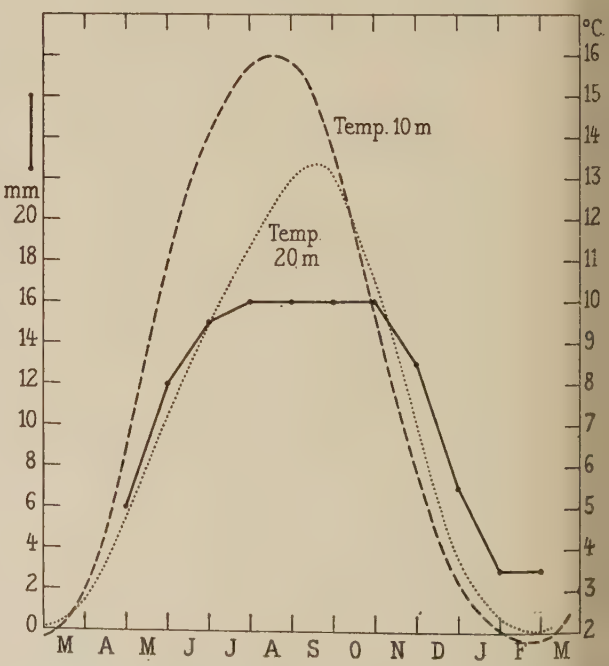


Fig. 2. Monthly growth of transplanted North Sea plaice in the southern Little Belt compared with the mean temperature at the station "South of Fyn", 10 and 20 m. depth.

The length of plaice of the youngest age-groups ermined at fishing experiments carried out by Danish Biological Station is — after correction the plaice measured to the cm. below — at the l of the growth-year as follows[2]):—

	Aalbæk Bay Herthas Flak (northern Kattegat) Depth 5–35 m.	Southern Kattegat and the Belt Sea	Western part of the Baltic proper
gr.	8·5 cm.	10·5 cm.	9·5 cm.
r.	15·0 cm.	18·5 cm.	16·0 cm.
gr.	22·5 cm.	ca. 26 cm.	23·5 cm.
-gr.	ca. 26 cm.	ca. 30 cm.	

The growth of the local as well as of the trans- nted plaice in the Belt Sea has in recent years en closely followed through marking experi- nts, and H. Blegvad has issued a very ailed report on the results of these experiments *c. cit.*). The length of the plaice marked during 29—1933 varied between 20 and 25 cm.; average ·4 cm. The growth of plaice, liberated in the ferent areas[3]), was as follows:—

Growth in 1st year after marking.

		local	transplanted
erated	North of Fyn	7·8 cm.	11·9 cm.
„	Little Belt	8·3 „	12·3 „
„	South of Ærø	9·4 „	ca. 13·3 „
„	Great Belt	9·4 „	12·4 „
„	Sejrø Bay	9·4 „	12·5 „
„	Smaalands Sea	9·7 „	12·0 „

Causes of local Differences in Growth.

As we know the growth is dependent on the nsity of the stock; great density means less food r fish and therefore slower growth. In the lbæk Bay—Herthas Flak area the stock of plaice ten times as dense, and the stock of dabs which serious competitors with the plaice for food out twice as dense as in the Belt Sea. Further find here a considerable number of competitors r food among the invertebrates (*Asterias rubens*, *ssa reticulata*, and others). We therefore find a w rate of growth here. The competing inverte- ates which are fairly rare in the Belt Sea must considered a factor of importance in the ttegat.

Within the Belt Sea the differences in total arly growth are fairly small. The growth seems he slowest in the area north of Fyn both as gards the local and the transplanted plaice. A mparatively low summer temperature of the per layer is a special feature of this area. This caused by an especially strong admixture of water from the lower layers of the Kattegat (J. P. Jacobsen, p. 24)[4]).

The course of the growth-curves must, however, necessarily depend to some extent on the nature of the fishery. In the growth-curves published by Dr. Blegvad for local and transplanted plaice it is shown that the maximum growth-rate is reached later in some places than in others. The growth-curves for the Great Belt and the Sound take a somewhat different course from those for other areas. The maximum growth is here reached late, but when it comes the rate of increase is, in return, faster than in any other area. As regards the Great Belt the explanation is this that during the first months after the marking especially large numbers of recaptures are made here in set nets close to the shore (See H. Blegvad, *loc. cit.*, p. 27). The smallest fish have a tendency to move coastwards. Their liability to recapture is therefore greatest and the average length of the recaptured fish in the early months has consequently been remarkably low. The remaining stock of marked fish, on the other hand, has contained the larger fish, a fact which explains the apparent great increase in the growth.

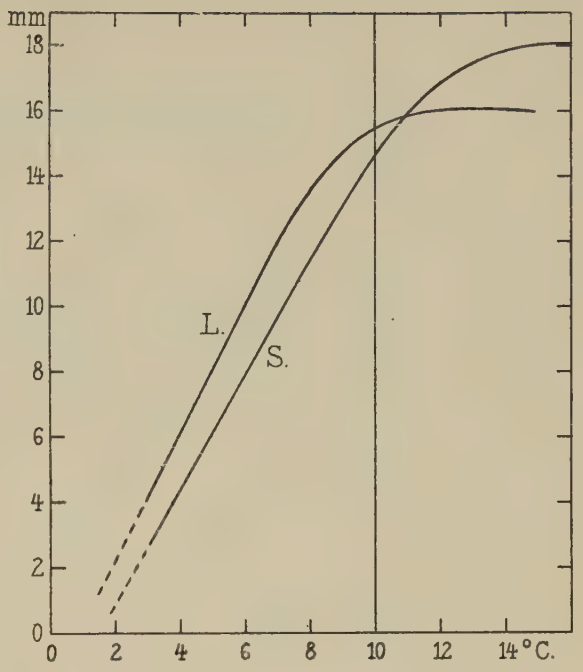


Fig. 3. Connexion between temperature and monthly growth of transplanted North Sea plaice in the Sejrø Bay, S.-curve (cf. Fig. 1), and the southern Little Belt, L.-curve (cf. Fig. 2), respectively.

[2]) Aage J. C. Jensen, Investigations on the Stock of ice in the Kattegat and the Belts in the Years 1927—29. Rapp. et Proc.-Verb., Vol. LXXI, 1931.

[3]) Partly recaptured in other areas (H. Blegvad, *.cit.*, p. 71 *et seq.*).

[4]) J. P. Jacobsen, Mittelwerte von Temperatur und Salzgehalt. Medd. Komm. f. Havunders., Ser. Hydrografi, Bd. I, No. 10, 1908.

Fig. 4. Chart of the Kattegat and the Belt Sea.

The same phenomenon probably occurs in the ound, but the low salinity of the upper layer there without doubt another factor of importance. his causes especially the transplanted fish to keep the lower layer where the temperature rises more owly in the spring.

It may be noticed from the above growth-table hat in the Smaalands Sea, the shallowest area where the depth only in a small channel in the estern part exceeds 15 m.) and where the salinity always comparatively low, the greatest growth or local plaice, but the smallest growth for trans-lanted plaice is recorded.

Up to about 10° C. the growth is in linear roportion to the temperature, above this degree increases but little.

In Figs. 1 and 2 the average monthly growth f transplanted plaice in Sejrø Bay and Little Belt compared to the temperature of the water. The onthly growth-curves are based on the growth-urves given by Dr. B l e g v a d (*loc. cit.*, Fig. 33). n the shallow Sejrø Bay area the growth follows ne temperature of the water at a depth of about 0 m. (the temperature curve is taken from Schultz' Grund" L. V., 10 m.). In the Little Belt rea where the depth is largely above 15 m., and ven in a considerable section above 20 m., the rowth follows the temperature of the water at a epth of 20 m. (The temperature curves are taken rom a station south of Fyn at 10 and 20 m. The ourse of the temperature curve at a depth of 10 m. aries but little from the course of the correspond-ng curve from "Schultz' Grund" L. V. as shown n Fig. 1.)

It should be kept in mind that the growth does ot follow the change in temperature with com-lete accuracy as the depth at which the plaice are o be found varies with seasons, even in the two ist mentioned areas which show great similarity s regards depth (See H. B l e g v a d, *loc. cit.*, . 61). Especially in the early months the plaice ave been found at depths considerably less than 0 m.

It is most remarkable that the ratio growth/ emperature is about the same in spring and utumn. This fact shows that about the same mount of plaice-food is available at both these easons. This is not the case at overpopulated areas uch as, e.g., Horns Reef Area where the growth n the autumn is perceptibly less than in the spring.

The figures show that the monthly growth rate s not greatly increased when the temperature rises bove 10° C. It is most probable that the monthly rowth reaches its optimum at about 13°—15°. he material at present discussed is not extensive nough to form a basis for any accurate judgment n this point.

In Fig. 3 is shown, on the basis of Figs. 1 and 2, the connexion between temperature and growth. It appears to be different for the two areas, and this very important question should be the subject of further investigations.

Causes of Changes in Growth.

Within the Transition Area a section exists in the northern and western Kattegat where the lengths of the different age-groups have remained practically unchanged since the beginning of this century[5]). The explanation is this that already before the year 1900 the fishery was carried out with such intensity that the total yield of the fishery culminated, i.e., A. C. J o h a n s e n's "third stage" was reached. This means that the stock has been thinned to such an extent that the accumulated stock has practically disappeared and the density has been reduced to the point below which the growth-rate does not perceptibly increase[6]) by thinning. The comparatively low growth-rate at the young-fish grounds in the Aalbæk Bay—Herthas Flak area remains low for the very reason that the Danish "saving"-fishery does not reduce the stock of young fish.

In the southern Kattegat and the Belt Sea the average length of the age-group has, however, become substantially greater. In the northern Belt Sea and the Great Belt the average length of the II-group in September—March increased in the years from 1907—11 till 1927—29 from about 20·5 cm. to about 26 cm.; the average length of the III-group increased from about 26 cm. to about 30 cm., and in the southern Kattegat the increase was so great that the average length of the II-group in 1930 was greater than the average length of the IV-group in 1905—07[7]).

The change in the southern Kattegat I have explained, on a previous occasion, partly as a direct consequence of the thinning of the stock caused by the fishery, and partly as caused by a change in the numerical ratio between the North Sea plaice and the Baltic plaice to the effect that the North Sea plaice has now become numerically the stronger[8]).

As regards the Belt Sea we find a corresponding thinning of the stock, caused by the intensive fishery, and a change in the racial character of the plaice.

---

[5]) A a g e J. C. J e n s e n, *loc. cit.*, p. 35.
[6]) *loc. cit.*, p. 39.
[7]) *loc. cit.* p. 38.
[8]) *loc. cit.* p. 39.

16

FACTORS DETERMINING THE APPARENT AND THE REAL GROWTH.

BY

AAGE J. C. JENSEN.

I. Methods of determining the Growth.

THE growth of plaice and dab may be determined by means of 1. Marking experiments, 2. Measuring of otoliths, and 3. Age analyses of the stock.

1. The **marking experiments** cannot give an entirely true picture:

(a) if the fishery is carried out with varying intensity in areas where the growth of the plaice varies. It is obvious that most recaptures occurring in a area chiefly populated by the slowest growing among the marked fish, must give misleading results. This error may very likely occur in marking experiments with plaice in the Horns Reef area where the fastest growing fish leave the nursery grounds and largely migrate to areas where the fishery is hampered by stony reefs. In such cases it must be realized that the increase in growth found through the marking experiments is not a growth-increment of the stock as a whole but only for that part which exists in the area where mark-ind and recaptures have taken place.

(b) if the marking experiments have been made with fish below the size limit the fastest growing individuals will be the first victims to the fishery and recaptures will indicate too high an increase in growth at first. The remaining part of the marked fish — the slowest growing individuals — will later indicate too slow a growth.

2. In the **measuring of otoliths** and the calculation of the lengths of the different age-groups on the basis of the width of the growth-zones two difficulties present themselves:—

(a) The fishery always removes first the fastest growing fish within an age-group and as these have most likely grown fastest also through the previous age-groups the measurements of otoliths on the remaining stock will inevitably show too slow a growth.

(b) More important is the fact that the growth of the otoliths is not proportional to the growth of the fish. Fig. 1 shows the proportion in the Horns Reef area between the length of dabs and the length of the otoliths (right otolith measured). It will be seen that as the fish increase in length the growth-rate of the otolith decreases. The proportion between the length of the fish and that of the otolith varies, however, in the different individuals. A back-calculation of the length of the age-groups is thus difficult even if it is assumed that the ratio between the lengths of the fish and the otolith in a single individual is that shown by the mean curve in Fig. 1.

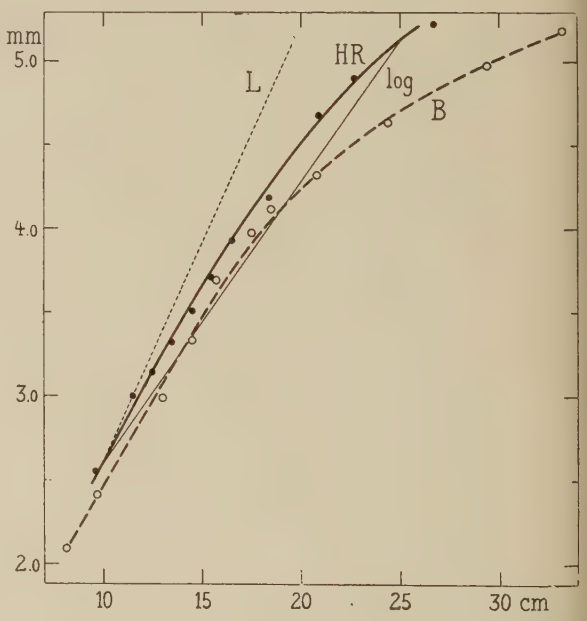


Fig. 1. Proportion between length of the dab and mean length of its otoliths in the Horns Reef area (curve HR), and in the Belt Sea and the Baltic (curve B) L representing the linear proportionality. The straight line "log" representing the ratio between length of otolith and logarithm of length of the fish for the Horns Reef area.

The error incurred by assuming linear proportionality between the lengths of the dab and otolith in the calculation of the length of the age-groups will in the case of dabs of a length of 25 cm. amount to about 3 cm. for the age-groups I and II.

This difficulty regarding measurements of the oliths of the dab, however, it seems possible overcome by means of a very simple re-calcu-ion, as the length of the otolith and the garithm to the length of the fish are, for all ractical purposes, in linear proportion (see Fig. at any rate as regards dabs between 10 and cm. in length.

A change in the ratio between the length of the h and that of the otolith seems to exist also as gards the plaice, although less pronounced.

The change is greatest in the caudal part of otolith, causing a steady increase in the centricity of the otolith with growth. In the case plaice otoliths it is, however, not possible to termine with accuracy the position of the centre nply by looking at it. By measuring the whole ngth of the otolith (right otolith) it has been und that the error incurred by assuming linear oportionality between the lengths of the plaice d the otolith in calculating the length of the unger age-groups amounts in plaice of about cm. length, from the Horns Reef area, to about m. for groups I and II.

3. **Age analyses of the stock.** The most usual thod of judging the growth of fish is the termination of the length of the age-groups from mples of the stock.

(a) Selectivity of gears. It is well own that great care must be taken to see that such mples have not been sorted by the fishing imple-nt. In commercial catches the fish are always ted, i.e., no fish below the size limit for commer-l fish are kept. The average length of those age-oups which are — more or less — the size limit ll, therefore, be found to be too great when nsidering only the specimens caught by the mmercial fishery. An example of the difference length of the age-groups of the plaice when ught in fine-meshed otter trawl at the scientific hing experiments and when caught in the Danish ne of the commercial fishery has been given by C. Johansen for 1909. The length of the group in September in a sample from the com-rcial fishery was then found to be 25·3 cm. ainst 22 cm. (about) determined by scientific hing experiments[1]).

In a sample of dabs caught by the commercial hery in the vicinity of "Graadyb" lightship in nuary the lengths of the age-groups as compared th the lengths found at fishing experiments with e meshed otter trawl in the southern Horns Reef ea in June after about 4 and 5 growth periods re as follows:—

In a sample from the commercial fishery[2]) Jan. 31, 1933.		In a catch with fine-meshed otter trawl June 1937.	
Growth period	Length in cm.	Growth period	Length in cm.
4	22·0	3½	16·6
5	24·0	4½	19·3

Thus, if we determine the average length of the age-groups in the Horns Reef area on samples caught with fine-meshed otter trawl we get an average length quite as low as that in the eastern Baltic. Unfortunately we find in the literature on the subject many inaccurate figures of growth due to selectivity of gears not being considered.

(b) The effect of the fishery on the length distribution of the age-groups. If at scientific fishing experiments the samples are taken with a sufficiently fine-meshed otter trawl and in such a way that samples are representative of the stock in its entire distribution the error, otherwise committed by assuming that a single section of an area of distribution contains a stock sufficiently representative of all the age-groups, is avoided.

Even so only an approximately accurate measure of the growth of the youngest age-groups is obtained. The effect of the commercial fishery in reducing the stock of members above the size limit is as regards the older age-groups considerable. This effect is apparent in the length distribution of the various age-groups.

The increase in length during growth is, when food conditions are the same, proportional to the original length of the fish. The general length distribution of an age-group is, therefore, not symmetrical but skew and it may be expected that it will approximate to the logarithmic distribution (i.e., the distribution of the logarithms is normal).

The degree of skewness may be calculated from the formula $S = \frac{\Sigma a^2}{n} : \sigma^3$; a being the deviation from the mean of the n variants, and σ being the standard deviation[3]).

For the southern Horns Reef area in 1936 and 1937 the following values for the skewness for groups I and II of plaice are found:—

	I-gr.	II-gr.
1936	1·56	0·12
1937	1·26	0·47

A skewness of less than 0·25 may be considered as being immaterial whereas a skewness above 0·50 is considerable.

It will be seen that the skewness of the I-group was considerable while that of the II-group was much less even though in 1937 not imperceptible. The length distribution is shown on Fig. 2.

[1]) A. C. Johansen, Bericht über die dänischen Untersuchungen über die Schollenfischerei und den Schollenbestand etc. — Medd. Komm. Havunders. Ser. Fiskeri, III. Nr. 8, 1910.

[2]) E. M. Poulsen, The dab in the Danish waters. — Rep. Dan. Biol. Stat. XXXVIII, 1933.

[3]) W. Johansen, Elemente der exakten Erblichkeitslehre. Jena, 1913, p. 244.

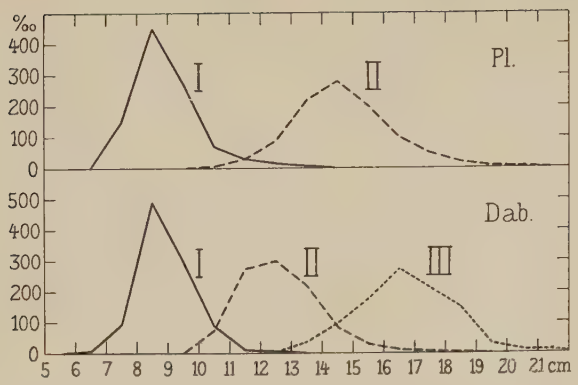


Fig. 2. Length distribution of the youngest age-groups of plaice (mean of 1936 and 1937) and dab (1937) in June in the southern Horns Reef area, between 5 and 30 m. depth.

As regards the dab the case is similar but the point at which the curve is influenced by the fishery occurs later, not until age-group III has been reached, on account of the slower growth of the dab and also on account of its more slender shape which enables it to escape through the meshes at a length at which the plaice would be caught. The degree of skewness for the dab in the southern Horns Reef area in 1937 was the following:—

I-gr.: ..... 0·59
II-gr.: ..... 0·72
III-gr.: ..... 0·16,

e.g., a very slight skewness of group III in contrast to the natural, great skewness of groups I and II. The length distribution of the dab is also shown on Fig. 2.

II. The Dependence of the Growth on the Temperature and the Amount of Food available.

The growth period of the plaice. The extensive experiments made by Ben Dawes regarding conditions of growth and maintenance of the plaice showed that the lowest limit for growth of plaice is at about 10°C. off Plymouth. It is, however, certain that this temperature limit varies in the different areas, and perhaps for the different races.

The rate at which the metabolism of the plaice takes place depends, as in the case of other cold-blooded animals, on the temperature, and the growth is therefore determined partly by the amount of food taken, partly by the temperature. Even where the best possible food conditions exist there will be an upper temperature limit at which the metabolism has reached its maximum where feeding cannot supply a surplus for growth. If we compare, for the experiments from Lympstone and Cawsand respectively, the mean values for increase in growth of the "maximum-feeding plaice", calculated from the values given by Ben Dawes for the separate fish[1]), with the temperature we see that the growth increases proportionally with the temperature only up to about 14°—15° and that above about 15° there is a tendency towards a decrease (see Fig. 3).

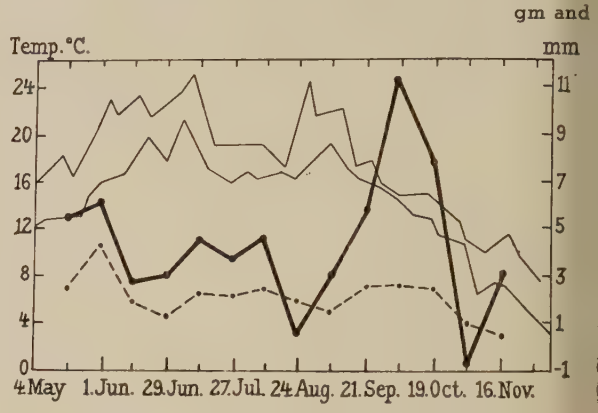


Fig. 3. Mean length increment of maximum-feeding plaice in fourteen-day periods at the Lympstone experiments of 1930 (from Tables by Ben Dawes, 1931) showing negative correlation between growth and temperature at temperatures above some 15° C.

Upper curves: Maximum and minimum temperatures, respectively.
Broken line: 14-days increase in length in mm.
Heavy line: 14-days increase in weight in g.

It must be remembered that it is the increase in weight and not in length which must be compared with the variations in temperature as the increase in weight at a growth of 1 cm. is about 60 % greater at a length of 24 cm. than at a length of 20 cm.

When we regard the growth in the Horns Reef area at the beginning of this century as shown in the records of the marking experiments carried out at that time we find that the growth-rate reached a pronounced maximum about July—August when the temperature of the water was about 12°—15° and that a decrease in the growth-rate took place during the following months when the temperature of the water culminated (in August and the first part of September) and this decrease continued into the autumn and winter (see Fig. 3). In this densely populated area the growth was apparently checked in the course of the growth-period because the amount of food available was gradually reduced.

From the extensive marking experiments in the Belt Sea on plaice transplanted from the Horns Reef area it is seen that the growth-curve here closely follows the curve of the temperature of the water except that here too the growth does not increase at above some 15°C.

[1]) Ben Dawes. Growth and Maintenance in the Plaice. (*P. platessa*, L.) Part. II. Journ. Mar. Biol. Assoc., Vol. XVII, No. 1, 1930.

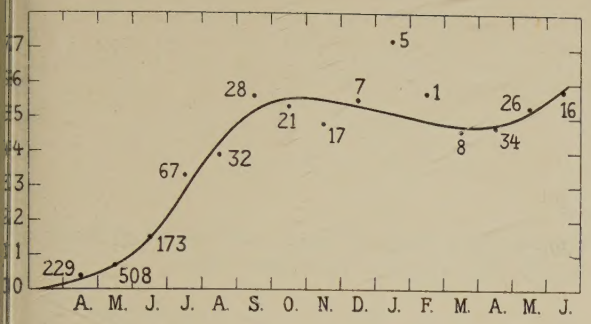


Fig. 4. Length increment of plaice marked during March—April 1903—12 at recapture in the different months.

Fig. 4 shows that the length of the plaice caught in March—April is less than that of those caught the previous autumn. The cause of this is probably to a great extent migrations and seasonal changes of the fishing grounds, but an additional cause is probably the fact that the fastest growing fish are first caught by the fishery with the result that the average length of the remaining fish, which grow but little in the winter, is reduced.

The fact that the marking experiments do not show the real growth because the fastest growing of the marked fish are first removed — with the result that the marking experiments show too small a growth increment — makes itself still more felt now in the Horns Reef area when the present intensity of the fishery is so much higher than before. This is undoubtedly the cause of the very slight yearly increase of 2—3 cm. which the marking experiments now show although the increase undoubtedly to-day is less than in the years 1903—1912.

III. Phaenotypes of Plaice in the North Sea.

The occurrence of different races of food fish has been studied extensively as regards most of species. In these investigations the aim has been to study the more genotypically defined characteristics rather than the phaenotype. The study of the phaenotype is, however, of great practical value as it is the phaenotype which affords the truest picture of the conditions in which the fish lives its life, and more especially the conditions which determine its growth.

The difference in shape between the slow growing, slender, large-headed North Sea plaice

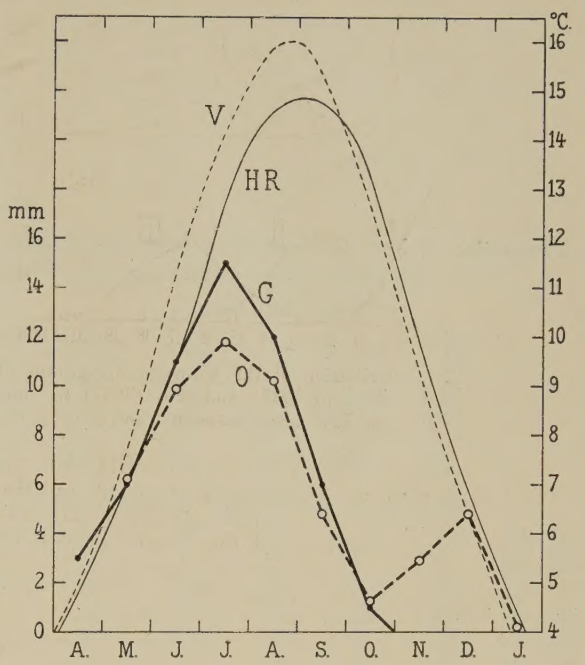


Fig. 5. Monthly growth of plaice, G and O, in the Horns Reef area according to marking experiments 1903—12 compared with bottom temperature at "Vyl" L. V., 22—23 m. depth, (curve V) and "Horns Reef" L. V., 32 m. depth (curve HR), respectively.

G: Monthly growth from the smoothed curve in Fig. 4.
O: Monthly growth from original measurements on recaptured plaice smoothed for each successive 2½ months.

from the Horns Reef area and the fastgrowing Belt Sea plaice is well known. In Rep. Dan. Biol. Stat. Vol. XXXVIII, Dr. Blegvad has illustrated extreme types. There is, however, in the North Sea itself considerable difference in the shape of the plaice, as is seen from Table 1 below. The most slender form and the largest head was found in the plaice from the most densely populated of the areas investigated, i.e., the Horns Reef area.

That the shape is something markedly phaenotypical, obviously closely connected with the food conditions, is proved by the fact that plaice which have been transplanted from the Horns Reef area to the Belt Sea gradually approach the shape of the native Belt Sea plaice (see Table 1), becoming rounder and less large-headed.

Table 1 on next page.

Table 1.

Proportion 1) between height of body and length, and 2) between lengt of head and height of body of plaice in different parts of the Southern North Sea and the Transition Area.

	Horns Reef Area												
	North H.R. 18 m.	Southern H. R. 24—26 m.	Southern H. R. 12—22 m.	North H.R. 16—17 m.	N. & S. H.R. 14—23 m.	Off W. coast 56°11'N.L. 17 m.	Indefatigable Bank 17—37 m.	N.W. of Heligoland 37 m.	Skagerak off Hirtshals 16—22 m.	Belt Sea Sound E. of Sjælland	Great Belt and Little Belt		Belt Sea and E. of Sjælland
											Baltic plaice	North Sea race	
	May 1932	June 1936	June 1936	June 1936	June 1937	June 1936	June 1937	June 1937	July 1930	Aug. 1930	Nov.-Dec. 1933		Apr.-May 1937
	Height in percentage of total length.												
30—31	—	—	—	—	1	—	—	—	—	—	—	—	—
32—33	1	4	7	7	3	—	—	—	—	—	—	—	—
34—35	17	59	77	81	12	9	3	—	9	—	—	1	—
36—37	39	46	71	91	17	7	13	10	22	1	—	—	5
38—39	17	1	11	10	4	3	4	17	27	3	4	7	17
40—41	1	1	—	—	2	1	—	4	5	12	17	16	17
42—43	1	—	—	—	—	—	—	—	—	6	16	15	7
44—45	—	—	—	—	—	—	—	—	—	3	12	1	3
46—47	—	—	—	—	—	—	—	—	—	1	2	—	—
Total	*76*	*110*	*166*	*189*	*39*	*20*	*20*	*31*	*63*	*26*	*51*	*40*	*49*
Mean	37·1	35·8	36·0	36·1	36·3	36·6	37·1	38·6	37·8	41·7	42·7	41·3	40·5
	Length of head in percentage of height of body.												
40—42	—	—	—	—	—	—	—	—	—	2	—	—	—
43—45	—	—	—	—	—	—	—	—	—	5	7	—	—
46—48	—	—	—	—	—	—	—	—	—	8	15	8	2
49—51	—	—	—	—	—	—	—	—	2	7	21	14	11
52—54	1	—	—	—	—	—	—	1	5	1	7	15	15
55—57	3	1	—	2	1	2	1	7	12	1	—	3	3
58—60	5	2	12	13	3	1	7	14	22	—	—	—	6
61—63	21	22	35	28	12	5	8	7	14	—	—	—	2
64—66	28	42	50	74	15	7	3	2	3	—	—	—	—
67—69	17	33	49	58	3	4	1	—	2	—	—	—	—
70—72	—	7	16	13	2	1	—	—	3	—	—	—	—
73—75	—	3	3	1	3	—	—	—	—	—	—	—	—
76—78	—	—	1	—	—	—	—	—	—	—	—	—	—
Total	*75*	*110*	*166*	*189*	*39*	*20*	*20*	*31*	*63*	*24*	*50*	*40*	*39*
Mean	64·5	66·4	66·2	66·1	65·3	64·4	62·3	59·3	61·1	47·6	49·2	51·8	53·9